UNIVERSITÉ DU QUÉBEC À RIMOUSKI

ÉTUDIER LE FONCTIONNEMENT DE L'ÉCOSYSTÈME BENTHIQUE DE ZONES CONSIDÉRÉES COMME DES *HOTSPOTS* ET *COLDSPOTS* DE L'ARCTIQUE CANADIEN

STUDYING THE FUNCTIONING OF BENTHIC HOTSPOT AND COLDSPOT ECOSYSTEMS IN THE CANADIAN ARCTIC

Thèse présentée

dans le cadre du programme de doctorat en océanographie

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PAR

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Composition du jury :

Gustavo Ferreyra, président du jury, Université du Québec à Rimouski

Philippe Archambault, directeur de recherche, Université du Québec à Rimouski

Dieter Piepenburg, codirecteur de recherche, Universität Kiel, Allemagne

Ursula Witte, examinatrice externe, University of Aberdeen, UK

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Meinen Eltern

Man holt aus dem Leben das Beste heraus, wenn man das tun kann, was man gerne tut.

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AVANT-PROPOS

This thesis 'Studying the functioning of benthic hotspot and coldspot ecosystems in the Canadian Arctic' is focused on the description and understanding of patterns and processes at the Arctic seafloor, and how different factors can influence them. The ultimate motivation is the need to find methods, possibly sentinel sites, at which we can monitor how global changes influence the Arctic benthic ecosystem and relate these to the entire ecosystem. Moreover, the Convention on Biological Diversity has called for the definition of 'Ecologically and Biologically Significant Areas' (EBSAs) by each country in its territory as a baseline for sustainable use and development in the future.

Establishing baseline data on benthic functions from several years and across the Canadian Arctic has only been possible through my active collaboration and participation in the following four research networks and projects:

Canadian Healthy Oceans Network (CHONe, NSERC Strategic Network)

CHONe's research is focused on marine biodiversity and its role and use for sustainability of Canada's three oceans (Snelgrove et al., 2012). Expeditions were in collaboration with ArcticNet.

ArcticNet (Network of Centers of Excellence of Canada)

ArcticNet aims to study the impacts of climate change in the coastal Canadian Arctic and helps to bring researchers, Northerners and managers from different fields together.
Expeditions: 04/09/2008 – 05/10/2008 (Lancaster Sound, Baffin Bay)
08/10/2009 – 06/11/2009 (Beaufort Sea to Labrador coast)

International Polar Year – Circumpolar Flaw Lead Study (CFL)

The CFL study aimed to gain a better knowledge, how changes in the flaw lead system, areas of thinner or open ice in the Arctic, affect physical and biological processes (Deming and Fortier, 2011). Expedition: 03/06/2008 – 07/06/2008 (Beaufort Sea)

Malina

The Malina project studied how changes in permafrost, ice cover and light penetration influence biological diversity and biogeochemical fluxes of the Arctic Ocean. Expedition: 30/07/2009 – 27/08/2009 (Beaufort Sea)

While CHONe has been the major source of financing for this thesis, in the following I present how my work contributed to the different objectives of all networks/projects. The table below shows, which chapter of my thesis contributes mostly to which network/project. It also gives an overview of other collaborative publications, which I co-authored during my thesis, and conferences and meetings of the respective network/project, in which I participated with oral or poster presentations

<table>
<tr><th></th><th>CHONe</th><th>ArcticNet</th><th>CFL</th><th>Malina</th></tr>
<tr><td rowspan="4">Publications & scientific manuscripts</td><td colspan="2">Link et al. (chapitre 4)</td><td>Link et al. (2011, chapitre 1)</td><td>Link et al. (chapitre 2)</td></tr>
<tr><td>Link et al. (chapitre 3)</td><td colspan="2">Darnis et al. (2012)</td><td rowspan="3">Rontani et al. (2012)</td></tr>
<tr><td rowspan="2">Kenchington et al. (2011)</td><td rowspan="2">Fortier et al (in press)</td><td>Tremblay et al. (2011)</td></tr>
<tr><td>Forest et al. (2011)</td></tr>
<tr><td rowspan="7">Related conferences and meetings</td><td>CHONe 2009</td><td>Expedition planning 2008</td><td rowspan="7">All-Hands CFL 2009</td><td rowspan="7">Plenary meeting 2010</td></tr>
<tr><td>Hermione 2011</td><td>Arctic Change 2008</td></tr>
<tr><td>CHONe 2011</td><td>Expedition planning 2009</td></tr>
<tr><td>CSAS Arctic EBSAs 2011</td><td>ArcticNet ASM 2009</td></tr>
<tr><td rowspan="2">WCMB 2011</td><td>ArcticNet ASM 2010</td></tr>
<tr><td>IPY 2012</td></tr>
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Notably, I participated in the Scientific Advisory Process by the Canadian Science Advisory Secretary for the definition of EBSAs in the Canadian Arctic. For this, we prepared a comprehensive research document on benthic EBSAs in the Canadian Arctic (Kenchington et al., 2011). Chapitre 3 of my thesis summarizes benthic remineralisation flux data that has been published as part of collaborations with Kenchington et al. (2011) and Darnis et al. (2012).

Although my passion and expertise is the invertebrate life at the seafloor, I consider it an important mandate to communicate and integrate my research findings into the bigger picture. I am therefore grateful for the opportunities mentioned above. I sincerely hope that my efforts can accelerate the process of taking the scientific results presented in this thesis on to its application in the sense of the original motivation.

LIST OF PUBLICATIONS FROM MY THESIS WORK

Link, H., Archambault, P., Tamelander, T., Renaud, P.E., Piepenburg, D. (2011, chapitre 1) Spring-to-summer changes and regional variability of benthic processes in the western Canadian Arctic. Polar Biology. 34(12): 2025-2038.

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Link, H., Piepenburg, D., and Archambault, P. (chapitre 4) Are Hotspots always hotspots? Temporal variability and its role for the relationship between diversity and ecosystem functioning in Arctic benthic environments. For submission in PLoS ONE

Darnis, G., Robert, D., Pomerleau, C., Link, H., Archambault, P., Nelson, R., Geoffroy, M., Tremblay, J.-É., Lovejoy, C., Ferguson, S., Hunt, B., and Fortier, L. (2012) Current state and trends in Canadian Arctic marine ecosystems: II. Heterotrophic food web, pelagic-benthic coupling, and biodiversity. Climatic Change 115: 179-205.

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Tremblay, J.-É., Bélanger, S., Barber, D., Asplin, M., Martin, J., Darnis, G., Fortier, L., Link, H., Gratton, Y., Archambault, P., Sallon, A., Michel, C., Williams, W., Gosselin, M., Philippe, B. (2011) Climate forcing multiplies biological productivity in the coastal Arctic Ocean. Geophysical Research Letters. 38, L18604

LIST OF PRESENTATIONS FROM MY THESIS WORK

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Link, H.*, Piepenburg, P., Archambault, P. (2009) Hotspots in the Cold - Patterns of benthic carbon turnover in the Canadian Arctic. CHONe Network Meeting, Montreal, Canada, 1 - 3/10/2009. (Poster, Award)

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RÉSUMÉ

L'océan Arctique est de plus en plus affecté par les changements climatiques et les intérêts économiques de l'humanité. Le développement durable de l'Océan Arctique ne saurait se faire sans une évaluation exhaustive et rapide de son écosystème et de son fonctionnement. La dégradation de la matière organique sur le fond de l'océan engendre des flux d'oxygène et de nutriments liés aux cycles biogéochimiques du système marin global. Ultimement, cette reminéralisation benthique participe à la production primaire dans les couches de surface de l'océan. Nos connaissances sur la diversité, la physique et la chimie de l'Océan Arctique se sont améliorées, mais nous en savons toujours très peu sur le fonctionnement de l'écosystème benthique. Le but de cette thèse est donc la description et la compréhension du fonctionnement de l'écosystème benthique et de sa variabilité à des '*hotspots*' et '*coldspots*' en Arctique canadien. Plus précisément, je me suis intéressée à comprendre comment les ressources alimentaires, la diversité et autres paramètres environnementaux influencent la reminéralisation benthique et ce, à différentes échelles spatiales et temporelles. Pour cela, j'ai effectué des incubations de carottes de sédiment provenant du milieu naturel; ces incubations ont été faites en milieu contrôlé sur des bateaux. J'ai échantillonné plusieurs sites, sur deux années et trois saisons, pour déterminer la quantité de pigments dans les sédiments, les flux d'oxygène, de nitrate, de nitrite, de phosphate, d'acide silicique et d'ammonium. J'ai également identifié la macrofaune présente dans ces carottes de sédiment.

Dans le chapitre 1 de ma thèse, j'ai étudié l'influence de la transition saisonnière printemps-été dans le sud-est de la mer de Beaufort sur la reminéralisation benthique du carbone et ses facteurs déterminants, c'est-à-dire les ressources alimentaires et la biomasse de l'endofaune. Les résultats ont montré qu'il y a des changements saisonniers de la reminéralisation benthique et de la quantité de pigments sédimentaires, mais pas de la concentration de Chl *a* et de la biomasse de l'endofaune. Dans les deux saisons, la concentration de Chl *a* dans les sédiments est le facteur le plus important pour expliquer la variation spatiale de la reminéralisation, mais au printemps, la profondeur des sites est aussi un facteur explicatif, alors qu'en été, c'est la biomasse de l'endofaune. Mes résultats révèlent un effet combiné et dynamique de la situation alimentaire et de la communauté benthique sur la reminéralisation benthique du carbone.

Mon deuxième objectif était de déterminer l'influence de paramètres abiotiques et biotiques, lesquels varient sur des échelles temporelles différentes, sur la variabilité spatiale de flux de reminéralisation multiples (chapitre 2). Des analyses multivariées ont démontré que les flux d'oxygène, qui sont généralement utilisés comme un proxy, ne peuvent pas expliquer la variation spatiale de l'ensemble des flux de reminéralisation

benthique. J'ai également testé l'influence des paramètres environnementaux suivants sur les flux benthiques: flux verticaux de carbone organique en particules, concentration de Chl *a* dans les sédiments de surface (échelle court-terme), porosité, concentration de manganèse et fer en surface des sédiments, concentration d'oxygène en eau profonde (échelle long-terme), phaeopigments (échelle intermédiaire) et $\delta^{13}C_{org}$ (influence terrestre). La variation spatiale de l'ensemble des flux est expliquée le mieux par la concentration de Chl *a*, les phaeopigments, $\delta 13C_{org}$, et le manganèse en surface des sédiments et par l'oxygène en eau profonde. Alors, c'est notamment les paramètres environnementaux qui expliquent le plus le patron spatial de flux multiples, mais l'historique d'apports en matière organique et l'influence terrestre peuvent modifier ce patron.

Dans le chapitre 3, je donne une vue d'ensemble des données sur les flux benthiques multiples qui ont été publiées ou compilées pendant ma thèse. J'étudie la localisation géographique en Arctique canadien des *hotspots* et des *coldspots* de reminéralisation benthique; le plateau peu profond de Mackenzie, le détroit de Lancaster et la polynie du Nord sont des *hotspots*. Ma participation à la description '*Ecologically and Biolgically Significant Areas*' en Arctique canadien démontre qu'il est possible d'appliquer des données biogéochimiques dans le cadre d'évaluations d'écosystèmes à grande échelle.

Finalement, j'ai testé les hypothèses suivantes : (1) la variabilité annuelle de la reminéralisation benthique et de (2) la situation alimentaire est plus élevée à des sites *hotspots* que *coldspots*, (3) la composition taxonomique et (4) fonctionnelle des communautés benthiques ne change pas significativement entre les années et (5) la situation alimentaire explique la variation de reminéralisation benthique à une échelle temporelle, puis la diversité l'explique à une échelle spatiale (chapitre 4). Mes résultats supportent ces hypothèses et indiquent que les ressources alimentaires et la diversité benthique sont complémentaires pour l'explication de la variation de la fonction de reminéralisation benthique.

Globalement, je présente ici la première description de la fonction multiple en reminéralisation benthique à des *hotspots* et *coldspot* en Arctique canadien. Mes résultats démontrent que la relation entre la diversité et les fonctions de l'écosystème en milieu benthique arctique dépend fortement des ressources disponibles. J'ai également pu montrer que les effets interactifs de la variation spatio-temporelle peuvent cacher la détection des changements progressifs, particulièrement à des sites *hotspots*. Pour étudier les changements de diversité et de ressources alimentaires, il est necessaire de désigner des sites sentinelles à des *hot-* et *coldspots*.

Mots clés : Arctique, fonctionnement de l'écosystème, reminéralisation benthique, diversité, *hotspots*, flux, Chl *a* dans les sédiments, variation spatio-temporelle

ABSTRACT

Climate change and human interests are having increasing impacts on the Arctic Ocean. A profound and rapid assessment of its ecosystems and its functioning is essential, if we want development to be sustainable and maintain a healthy state of the Arctic Ocean. The degradation of organic matter at the seafloor effects oxygen and nutrient fluxes that are part of the biogeochemical cycles in the overall marine system. Thus, this benthic remineralisation eventually fuels primary production in surface waters. While inventories of diversity, physical and chemical parameters in the Arctic are improving, we still know little about the benthic ecosystem functioning. The aim of this thesis is to provide a description and understanding of benthic ecosystem functioning and its variability at hotspots and coldspots in the Canadian Arctic. More specifically I studied, how food availability, diversity (taxonomic, functional, abundance or biomass) and other environmental factors influence benthic remineralisation at different temporal and spatial scales. I used ship-board microcosm incubations of sediment cores from different sites in two years and three seasons to determine fluxes of oxygen, nitrate, nitrite, phosphate, silicic acid and ammonia as well as the inhabiting macrofauna. At the same sites I determined sediment pigment concentrations.

In chapitre 1 of my thesis I asked how the spring-to-summer transition influences benthic carbon remineralisation and its potential determining factors, food supply and infaunal biomass, in the southeastern Beaufort Sea. I found that benthic remineralisation and food supply patterns vary on the seasonal time scale, although infaunal biomass and sediment Chl *a* concentration does not. In both spring and summer, sediment Chl *a* concentration is the prime determinant of benthic carbon remineralisation, but other factors have a significant secondary influence, such as water depth (in spring) and infaunal biomass (in summer). These findings indicate the importance of the combined and dynamic effects of food supply and benthic community patterns on the carbon remineralisation.

My second objective was to determine the influence of biotic and abiotic environmental parameters, that vary on different time scales, on the spatial variation of multiple benthic remineralisation fluxes (chapitre 2). Multivariate analysis of flux data showed that the commonly used proxy (oxygen flux) does not explain overall variation in benthic remineralisation. I tested the influence of the following environmental parameters on benthic fluxes: vertical flux of particulate organic carbon, sediment surface Chl *a* (both short-term), porosity, surface manganese and iron concentration, bottom water oxygen (all long-term), phaeopigments (intermediate-term influence) and $\delta^{13}C_{org}$ (terrestrial influence). The overall spatial distribution of fluxes can be best explained by sediment Chl *a*, phaeopigments, $\delta^{13}C_{org}$, surficial manganese and bottom-water oxygen concentration. This indicates that environmental parameters of short time variation are most important for

spatial patterns of multiple fluxes, but also that historical input of organic matter and terrestrial influence can modify benthic remineralisation patterns.

In chapitre 3 I give an overview of all data on multiple benthic fluxes published in connection with and compiled during my thesis. I asked, where in the Canadian Arctic are hotspots - and coldspots - of benthic remineralisation function. The shallow Mackenzie Shelf, Lancaster Sound and the North Water Polynya present benthic remineralisation hotspots. The successful participation in the description of Ecologically and Biologically Significant Areas in the Canadian Arctic shows how biogeochemical data can be applied in larger ecosystem assessments.

Finally, I tested the hypotheses that (1) interannual variability of benthic remineralisation function and (2) food supply at hotspots is higher than at coldspots, that (3) taxonomic and (4) functional community composition does not change significantly between years, and that (5) food supply explains variation in benthic remineralisation on the temporal scale, and diversity on the spatial scale (chapitre 4). My results support all hypotheses and indicate that resource availability and diversity are complementary for the explanation of variation in benthic remineralisation function.

Overall, I present the first description of multivariate benthic remineralisation functioning at hot- and coldspots in the Canadian Arctic. My results demonstrate that the diversity-ecosystem function relation in arctic benthic systems strongly depends on resource availability and that the interactive effects of spatio-temporal variation may hide the detection of progressive change particularly at hotspots. Sentinel sites studying diversity and food supply changes should therefore be implemented at hot- and coldspots.

Keywords : Arctic, ecosystem functioning, benthic remineralisation, diversity, hotspots, fluxes, sediment Chl *a*, spatio-temporal variation

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INTRODUCTION GÉNÉRALE

Global change is modifying the environment we live in and pushes humans towards new frontiers. One of the last frontiers on Earth is the Arctic Ocean, itself being affected by rapid climate change. The exploration of resources in the Arctic is already underway. Protecting hotspots - areas with higher ecosystem functions than the average - has been suggested to help maintain ocean health. But knowledge is lacking, where they are, how to find them, and how they differ from other regions - hereafter coldspots. A profound and rapid assessment of its ecosystems and their functioning is essential, if we want development to be sustainable while maintaining a healthy state of the Arctic Ocean.

1. ECOSYSTEM FUNCTIONING AND SERVICES

Ecosystem functioning describes the integrated sum of the processes performed by the biota encountered in a specified ecosystem. Stachowicz et al. (2007) define it as "aggregate or emergent aspects of ecosystems (e.g., production, nutrient cycling), carrying no inherent judgment of value". In this document, ecosystem functioning will include mechanisms that influence ecosystem functions, while ecosystem functions are quantifyable products (such as the amount of released nutrients). When ecosystem functions are associated with a value to human society, we speak of ecosystem services (Naeem et al., 2009). For example, forest growth can be seen as wood production and carries an economical value. From an integrated economical perspective, the knowledge about marine ecosystem functioning will be important for developing a guideline for the sustainable use of marine resources, which is necessary to ensure the coexistence of humankind and the ocean's biota as its food and pleasure source (Wolanski 2006).

Economical values are sometimes difficult to assign to biogeochemical cycles, but the complex web of interactions and energetic and trophic links makes biological production or decomposition part of the nutrient cycles (Naeem et al., 2012).

The theory of global stability assumes that an ecosystem will always need to return to its equilibrium stable state after a perturbation. However, according to Gray and Elliot (2009), marine systems are more likely to follow the theory of the neighbourhood stability, where the system may exist and switch to an alternative steady state after perturbation.

Following the idea of alternative steady states, perturbation such as climate change can cause an ecosystem to fall into a stable state with, e.g., changed diversity patterns – that may coincide with changes in ecosystem functions. It is therefore likely that climate change will provoke changes in ecosystem functions and services (Cardinale et al., 2012).

Benthic ecosystem functioning

The majority of ecosystem functioning research has been conducted in terrestrial environments (Naeem et al., 2012). From the marine perspective, benthic ecosystems provide a comparative approach because they share important processes with the terrestrial system, as for example the competition for space and the limited mobility in adult stages due to which they depend on local resources.

A large number of benthic habitats from intertidal to deep-sea, from rocky to soft bottom or from temperate to arctic can be distinguished. Algae can play an important role in benthic ecosystem functioning up to the maximum light penetration depth (between 50 – 150 m), but on the macroscopic scale, the seafloor is generally dominated by invertebrates (Jahnke, 2004).

Different ecosystem functions have been studied in different benthic systems. Production of biomass by macroalgae has been related to macroalgal species richness in the tropical intertidal (Bruno et al., 2006). Danovaro et al. (2008) studied biomass production

mediated by nematodes in the deep sea to show the importance of the diversity of trophic groups for ecosystem functioning. In hard-bottom environments, the stability of community composition has been investigated as a measure of resistance against invasion or environmental change (McCann 2000; Wahl et al., 2011). Besides trophic links and community interactions described by these functions, biogeochemical cycles are an important component of ecosystem structure (Naeem et al., 2012), and the mechanims driving (functioning) nutrient regeneration has received increasing attention in soft-bottom environments (Raffaelli et al., 2003, Godbold and Solan, 2009).

In benthic systems, nutrient regeneration is the release of nutrients from the sediments to the water column following the mostly bacterial degradation of organic matter. The degradation products – mostly carbon dioxide, nitrate, ammonium, phosphate and silicic acid – eventually replenish the pool of nutrients necessary for primary production in the surface layers of the ocean. Although microorganisms play a crucial role in the chain of chemical reactions, their abundance and activity is to a large part influenced by macrofaunal activity (Michaud et al., 2009; Hunter et al., 2012). The amount of nutrient release versus nutrient uptake depends on a number of factors and processes, including input of organic matter, faunal composition and the related bioturbation and spatial variability in sediment geochemical properties.

Due to the complexity of these processes, in field studies, researchers are often forced to reduce the number of considered function metrics to a selection. In the marine Arctic system, only the carbon cycle has been described with an integration of benthic remineralisation into the entire system (Stein and Macdonald, 2004), and some local attempts have been made for the nitrogen cycle (Rysgaard et al., 2004; Chang and Devol, 2009). To our knowledge, only one study in the Arctic has investigated the remineralsation of multiple nutrients so far (Rysgaard et al., 1998), and nutrient remineralisation was discussed seperately for each flux as opposed to a multivariate ecosystem functions description. Until the science community has completetly resolved all single nutrient cycles, such multivariate description is necessary to estimate the importance of benthic

remineralisation to the overall system in status evaluation reports. It remains to be answered, where, in the Arctic Ocean, areas of high benthic ecosystem functions can be found.

2. FACTORS RELEVANT FOR ECOSYSTEM FUNCTIONING

The pattern of ecosystem functions in a system depends on the temporal and spatial scales that are considered (Schmid et al., 2009; Cardinale et al., 2009), and it can be controlled by a variety of factors, such as resource availability and diversity (Hooper et al., 2005). However, most studies have focused on the relation between biodiversity and ecosystem functions, aiming to estimate the consequences of biodiversity loss (Hooper et al., 2012), and promoting the idea that hotspots of biodiversity are important for global ecosystem functioning (Myers, 2000). But proof of diversity's importance for marine ecosystem functions is still scarce.

Biodiversity and ecosystem functioning

In the face of decreasing biodiversity (Chapin III et al., 2000; Hooper et al., 2012), the interest in describing the role of biodiversity for ecosystem functioning has significantly increased during the last decades (Hulot et al., 2000; Loreau et al., 2002; Solan et al., 2009; Naeem et al., 2012).

Several models for the biodiversity – ecosystem function relationship have been proposed and discussed particularly in terrestrial ecology literature (Hooper et al., 2005). It has generally been accepted by the expert community that biodiversity does affect ecosystem functions, but there is still an ongoing debate on the underlying mechanisms and direction of the biodiversity – ecosystem function relationship (e.g. Loreau et al., 2002; Stachowicz et al., 2007; Naeem et al., 2009).

Part of the debate involves, how biodiversity is measured. Traditionally, the number of species, taxonomic richness, has been used to explain plant biomass production, but soon the concept of functional traits evolved, assuming that it is not the mere number of species, but rather their complementarity in mediating different functions or occupying different niches which are important for the total ecosystem functioning (Naeem et al., 2012). If species are complementary in their traits, ecosystem functions should increase linearly with species richness. If species are redundant in their functions, the relation between species richness and ecosystem functions can be asymptotic or show a rivet-like distribution (Loreau et al., 2002). Such redundancy could serve as an insurance against ecosystem functioning changes, if environmental change reduces biodiversity (Yachi and Loreau, 1999). Finally, some species can provide a very particular, idiosyncratic role for the ecosystem's functions not encountered in other species, thus that we speak of an identity effect of the species (Loreau et al., 2002). Biodiversity can also be measured as phylogenetic, genetic, landscape or other kinds of diversity (Naeem et al., 2012). However, hereafter I will only treat diversity in terms of taxonomic and functional group richness and community composition, which are within the scope of my thesis.

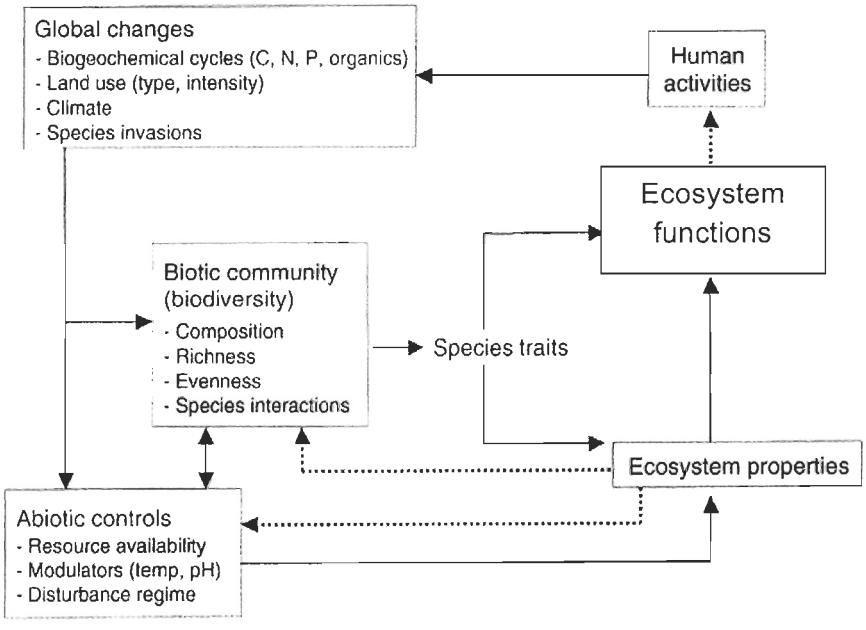

Fig. 1: Pathways and interactions of different factors influencing ecosystem functioning (modified from Hooper et al., 2005).

The concept of functional diversity has been helpful in the context of comparing the different models. There are several definitions of functional diversity: Steele (1991; Steele and Collie, 2004) refers to it as the variability of an ecosystem to respond to environmental changes. When working with biodiversity, however, the following definition is more appropriate and will be referred to hereafter: functional diversity describes the number of groups of species that share the same (relevant) traits of function. Commonly used traits to distinguish functional groups are, e.g., feeding mode (detritus vs. suspension feeder vs. grazer), lifespan, size, bioturbation type and mobility (Bremner et al., 2003). Working with functional diversity, e.g., avoids redundancy as a confounding factor for the analysis of how diversity influences ecosystem functions. It moreover allows the comparison of geographically distinct systems by introducing a 'standard' to the measurement of species. Functional diversity has also been a useful tool to refine ecosystem models without including the complexity of taxonomic diversity (Ebenhöh et al., 1995; Hulot et al., 2000; Steele, 2004).

In a study on the effects of diversity on nitrogen fluxes, Emmerson et al. (2001) found that a combined effect of idiosyncrasy and species diversity in different benthic macrofaunal assemblages provided the best explanation for variability in function. From another study, Bolam (2002) concluded that functional group richness is more important than species richness in benthic soft-bottom communities. Other extensive experimental studies including bioturbation and nutrient fluxes demonstrated that the functional group approach is useful for estimating the flux budgets when acknowledging geochemical properties of the habitat: The amount of organic matter recycled and nutrients remineralised in soft-bottom environments largely depends on the diversity and bioturbation identity of benthic communities (Pearson, 2001; Godbold and Solan 2009; Michaud et al., 2006; Michaud et al., 2009). But in Arctic benthic environments, diversity has rarely been linked to remineralisation function.

Resource availability and ecosystem functioning

Few studies within the diversity-ecosystem function debate have included the external factor resource availability to explain relationships. In fact, most studies are placed in experimental or controlled environmental settings, such that external variability cannot confound the diversity-ecosystem function relationship. However, in an experimental setup, Fridley (2002) found that resource availability dominates the relation between plant species richness and their production, and Cardinale et al. (2009) found important effects of resource availability on primary production patterns of phytoplankton species.

Contrary to experimental studies, observational studies are strongly influenced by the variability on the natural setting (Maestre et al., 2012). Non-intertidal benthic communities are supposedly limited by food supply from the water column (Jahnke, 2004; Klages et al., 2004). Hence, benthic activity may be greatly influenced by vertical flux patterns (Klages et al., 2004; Renaud et al., 2007a; Gradinger et al., 2010). Consequently, benthic remineralisation not only depends on the diversity of a benthic community, but also on the presence and quality of organic matter in the benthic environment (Sun et al., 2009).

Resource availability may also act indirectly on ecosystem functions (Fig. 1). Many studies have demonstrated that on a regional scale, diversity or abundance of communities increase with increasing quantity of food supply (Rex et al., 2006; Hoste et al., 2007; Witman et al., 2008). Thus, more resources would mean higher diversity, which increases ecosystem functions. Clearly, such interactions must be taken into account when looking for factors that can best predict areas of high ecosystem functions.

The influence of temporal and spatial variability in natural systems

Ecosystem functioning varies on the spatial (Glud, 2008; Schmid et al., 2009) and temporal scales (Yachi and Loreau, 1999; Farias et al., 2004; Frid, 2011). While experimental setups control for such confounding factors (or are specifically looking for it), spatio-temporal variation introduces an additional source of variation when studying the

influence of diversity and/or resource availability on ecosystem functions in the natural environment. For example, remineralisation in benthic environments is higher in summer than in winter (Renaud et al., 2007a), thus measures at different sites are comparable only in the same season. On the spatial scale, benthic remineralisation of nutrients is influenced by zonation of the redox-front in the sediments. In oligotrophic, well-oxygenated benthic environments, the oxic layer of the sediments can be several centimetres into the sediment. Thus, incoming organic matter is foremost aerobically remineralised and the sediments act as a source of most nutrients (Hensen et al., 2006). In less oxygenated sediments, the redox front can be closer to the sediment-water interface, and degradation of organic matter may require nitrate or even nitrite as reaction partner, thus that sediments in less oxygenated regions can act as a sink for nitrate (Hulth et al., 2005). The habitat precondition can affect how diversity of bioturbating macrofauna will be related to nutrient fluxes (Laverock et al., 2011).

The influence of temporal and spatial scales on ecosystem functions can also interact in their influence on variation. Benthic remineralisation of shallow water communities was different in one site of a lagoon than another, but only in one of two studied years (Thouzeau et al., 2007). This shows how seasonal differences can intervene if we want to generalize ecosystem processes from field study results.

Depending on the spatial and time scale observed, a measured change might therefore simply represent a stochastic change (the system will fall back to the equilibrium state), or a progressive change (the system will shift to another steady-state). To distinguish stochastic from progressive change, it is crucial to complete our knowledge on ecosystem processes with long-term studies including seasonal aspects as well as multiple spatial scales (Klages et al., 2004; Piepenburg, 2005; Stachowicz et al., 2007).

3. BENTHIC ECOSYSTEMS IN THE ARCTIC

Pelagic-benthic coupling and characteristics of the environment

Marine shelf ecosystems are characterized by a high turnover rate and close coupling between physical and biological processes. This is particularly pronounced in polar regions, where environmental factors such as ice-cover, light and temperature follow strong seasonal cycles. Primary production is mostly restricted to a limited period between April and September, when increasing light and decreasing ice-cover trigger the onset of biological cycles (Sakshaug, 2004). The greatest part of primary production is usually produced by the phytoplankton spring bloom in stratified waters after the ice-breakup in May-June, enhanced by high nutrient concentration built over the winter period (Arrigo and van Dijken, 2004; Carmack and Wassmann, 2006). But ice-algae and under-ice blooms may also contribute a significant component to the total production (Sakshaug, 2004; Mundy et al., 2009). Due to the intensity of spring blooms and ice-algae production, vertical fluxes may show significant export of organic matter to the seafloor, and we therefore generally speak of a high intensity of pelagic-benthic coupling in the Arctic (e.g. Piepenburg et al., 1997; Klages et al., 2004; Grebmeier et al., 2006a; Renaud et al., 2007b; Juul-Pedersen et al., 2008). The amount of exported matter depends on a number of water-column processes, most notably zooplankton grazing and microbial degradation. Timing of the bloom crucially influences the efficiency of secondary pelagic processes and thus the total amount of export (Forest et al., 2010).

Compared to the other world oceans, the Arctic Ocean (Fig. 2) is characterized by a particularly high amount of freshwater input via river runoff. The latter and high erosion rates along the coasts lead to a significant input of terrestrial material including organic matter (Klages et al., 2004; Macdonald et al., 2004). The Mackenzie River runoff located in the Beaufort Shelf region is the largest single sediment source in the Arctic Ocean (Macdonald et al., 2004) and leads to a high rate of terrestrial organic carbon burial compared to the marine organic carbon production in the Beaufort sediments (Goñi et al.,

2005). However, there is multiple evidence that the export of terrestrial organic matter does not provide a significant food source to benthic communities, probably due to its largely refractory quality (Rysgaard et al., 1998; Klages et al., 2004; MacDonald et al., 2010). Still, it influences the geochemical properties of sediments on a longer time scale (Gobeil et al., 2001).

Known patterns of benthic ecosystem functioning and its relation to resource availability and diversity in the Arctic

Processes in benthic ecosystem functioning in the Arctic follow the general patterns described for soft-bottom environments above. However, the peculiarities of polar environments also influence mechanisms in the benthos. Ice cover and seasonality in primary production combined with slowly onsetting zooplankton grazing is the cause for a very tight pelagic-benthic coupling in the Arctic compared to other marine regions (Fig. 3). This phenomenon is particularly pronounced along the marginal ice zone and polynyas, regions of physically induced open water surrounded by ice (Carmack and Wassmann, 2006). Accordingly, high benthic standing stocks have been recorded in corroboration of this theory on the Chuckchi Shelf (Grebmeier et al., 2006b), the North-East-Water-Polynya (Renaud et al., 2006), and the Barents Sea (Klages et al., 2004). The concentration of chlorophyll a (Chl *a*) in surface sediments – an indicator of detritus freshness, and therefore of tight pelagic-benthic coupling – has repeatedly been correlated with benthic carbon remineralisation (Renaud et al., 2007a,b; Carroll et al., 2008; Morata et al., 2008), and seems to be a better predictor than substrate heterogeneity (Piepenburg, 2005). One of the few studies on benthic carbon and nutrient remineralisation has been conducted in shallow sediments of an Arctic Fjord (Rysgaard et al., 1998). The authors found that nutrient release from the sediments increased markedly after the input of fresh organic matter, and a later study implied a positive influence of macrofauna bioturbation on sediment-water fluxes (Glud et al., 2000).

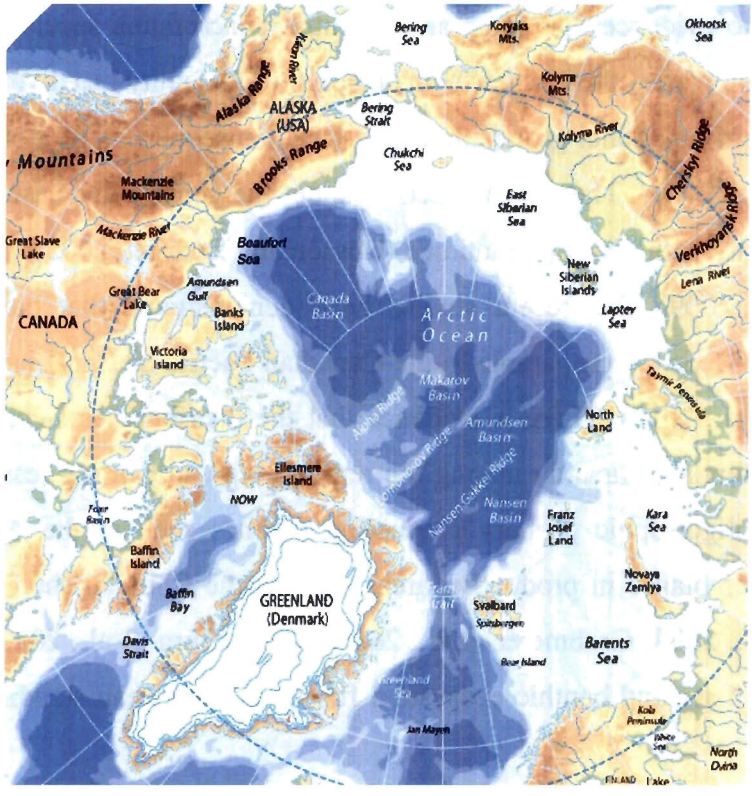

Fig. 2: Overview of the Arctic Ocean and adjacent seas. Map modified from AMAP (1998)

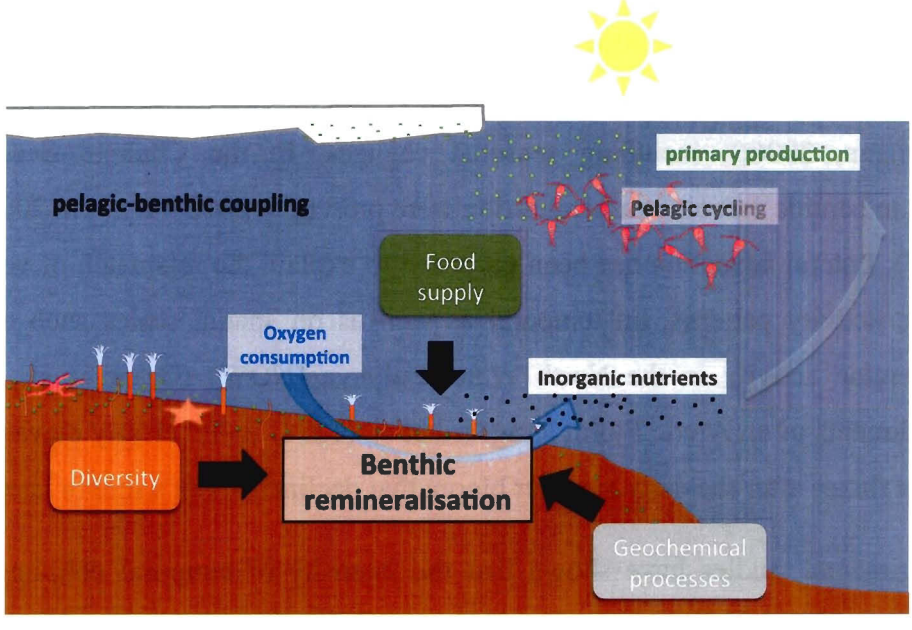

Fig. 3: Factors influencing benthic remineralisation in marine environments

There is also evidence that some arctic benthic macrofauna species prefer ice algae over phytoplankton while others ingest both, and that food quality has diverse effects on the activity of different functional groups, but long-term consequences of a change in diet are unclear (Sun et al., 2009). There is still debate about the general decrease of diversity and benthic productivity with increasing latitude (Cusson and Bourget, 2005; Piepenburg, 2005; Gray and Elliot, 2009). But recent studies have demonstrated that biodiversity in the Canadian Arctic Ocean is comparable to the Canadian Pacific or Canadian Atlantic Ocean (Archambault et al., 2010). There is evidence that the distribution of communities in the Arctic Ocean differs significantly among the regions, e.g., supporting less diverse benthic communities in oligotrophic primary production regimes such as the Arctic Basin, and more diverse assemblages in productive areas such as the Chukchi shelf and the Barents Sea (Klages et al., 2004; Grebmeier et al., 2006a; Piepenburg et al., 2011). However, the link between diversity and benthic ecosystem functions other than standing stock has not been studied.

Spatial and temporal variability of ecosystem functioning in the Arctic

Spatial and temporal variation of benthic carbon remineralisation has generally been coupled to vertical fluxes of organic matter in the Arctic (Grebmeier et al., 2006a; Carmack and Wassmann, 2006;), including seasonal changes. In the Chukchi Sea, seasonal differences in benthic carbon remineralisation were present in 2002 but not in 2004 (Lepore et al., 2007). Lateral advection has been proposed to explain the mismatch of vertical flux and benthic activity patterns, on temporal as well as on spatial scales such as the low reported benthic activity in the North Water Polynya (NOW) (Grant et al., 2002). In shallow sediments of an Arctic Fjord, Rysgaard et al. (1998) found clearly elevated oxygen and nutrient fluxes after the early summer bloom that declined about a month later.

Experimental studies have shown that the intensity of temporal coupling between food supply and benthic cycling can be in the range of hours to days (McMahon et al.,

2006; Sun et al., 2007), and the signal of a food pulse may be lost after a period of three weeks (Graf, 1992).

Recently, Grebmeier (2012) reported a possible progressive change in benthic community composition in the Bering Sea, but high temporal variability in the benthic biomass masked the statistical detection of the result.

These findings emphasize the importance of temporal variability in resource variability compared to spatial differences on benthic processes relevant for the marine carbon cycle in Arctic systems, but also the importance to better distinguish natural (oscillations) from induced (progressivly, driven by a factor) variability in benthic community patterns. Moreover, very little at all is known about nutrient remineralisation and the influence on it by benthic communities in these regions.

Known patterns of benthic ecosystem functions and food availability on the Canadian Arctic shelves

In the Canadian Arctic, benthic processes have been described most intensively from the CASES study on the Beaufort Shelf (2003-2004) and the NOW study in northern Baffin Bay (1997-1998), but the region is still understudied in the Arctic (Klages et al., 2004). With 90-175 g C m^{-2} y^{-1}, the Cape Bathurst Polynya is known for medium high primary production (Sakshaug et al., 2004), when compared to the more productive NOW (76 – 254 g C m^{-2} y^{-1}) (Klein et al., 2002). In contrast, benthic community oxygen demand was much higher in the Beaufort region than in the NOW (1.8 – 21.0 vs 1.7 – 4.1 mM O_2 m^{-2} d^{-1}) (Grant et al., 2002; Renaud et al., 2007b). On a regional scale, Renaud et al. (2007b) found highest influence of depth and food input on benthic oxygen demand. In both regions, single or three-site studies demonstrated important seasonal variation in benthic activity (Grant et al., 2002; Renaud et al., 2007a).

But neither the seasonal differences nor the striking differences in benthic activity between the western and eastern Canadian Arctic were reflected in Chl *a* distribution.

While the partitioning of oxygen demand between macrofauna and meiofauna and microbes was determined, a comparison with patterns in benthic biomass or diversity was not attempted so far.

Moreover, to my knowledge no data on nutrient remineralisation on Canadian Arctic shelves has been reported up to now, thus presenting a significant gap for nutrient budgets in the Canadian Arctic marine system.

Known patterns of diversity in the Canadian Arctic

Compared to benthic remineralisation, much more is known about benthic diversity in the Canadian Arctic, although large data gaps still exist, particularly when compared to other regions of the Arctic (Archambault et al., 2010; Piepenburg et al., 2011). In their review, Cusson et al. (2007) demonstrated that benthic assemblages differed among the seven regions on the Canadian Arctic shelf. A total number of 947 infaunal species and taxonomic groups were recorded, and taxonomic diversity was higher in eastern regions than in the central and western Canadian Archipelago.

In an extensive description of benthic communities on the Canadian Beaufort Shelf and Amundsen Gulf, Conlan et al. (2008) reported diversity to be high in general. The total number of taxa found was 497, and assemblages of different areas could be distinguished based on their composition, while composition differences were attributed mostly to water depth. The authors emphasized the relation between physical and environmental factors and the taxonomic composition of assemblages. They noted that different community composition might reflect differences in the system.

For the Lancaster Sound to Baffin Bay region, Thomson (1982) has reported similar patterns. He emphasized the abundance of suspension feeders vs. deposit feeders in shallow vs. deep environments, and again, depth and geographical location explained most of the variance in community composition assembled by the 343 taxa described from the study.

In the North Water Polynya (NOW), benthic diversity, composition, and feeding guild patterns identified three different communities, in the center, the east, and west of the polynya (Lalande, 2003). A total of 120 benthic taxa have been described, with particularly high abundance in the polynya center. Community patterns were related to sediment grain size, and only trophic organization was linked to food supply.

When comparing studies on benthic diversity in the Canadian Arctic Shelf, the following biodiversity hotspots have been described:

Lancaster Sound (Thomson, 1982): Macrofaunal abundance and taxonomic richness was highest when compared to regions west of Barrow Strait and east of Lancaster Sound.

North Water Polynya (Lalande, 2003): Individual abundance and species diversity was highest in the center of the North Water Polynya, but did not directly reflect sedimentation patterns.

Cape Bathurst and Mackenzie Canyon (Conlan, et al 2008): Abundance was highest with comparable diversity within the southwestern Beaufort Shelf region.

Considering the numerous evidences for the variability of the biodiversity - ecosystem function relationship demonstrated in the course of the introduction, the question now arises, whether diversity hotspots such as in the Canadian Arctic also represent hotspots of benthic remineralisation, and whether this pattern is stable on a temporal scale considering the important variation in food supply in the system.

Importance of finding hotspots of benthic ecosystem functioning in the face of a changing Arctic

Climate change is predicted to induce major shifts in Arctic ecosystem processes at an intermediate time-scale (ACIA, 2004; Gray and Elliot, 2009; Wassmann et al., 2011). In fact, dramatic changes in sea-ice cover, water surface temperature and precipitation have already been recorded during the last decade, and they seem to exceed long-term variations such as the North-Atlantic-Oscillation (Carmack et al., 1995; ACIA, 2004; Barber et al., 2009). The opening of the North-West-Passage and its relevance for global economy as well as the accessibility of further resources also create much anticipation among stakeholders in the global competion for exploitation. Protecting hotspots of the marine ecosystem can help to maintain its health, meaning a condition in which the marine ecosystem's services and benefits to humans are sustainable - from food such as shellfish to climate such as carbon uptake.

In polar areas, polynyas are considered hotspots of primary production and marine ecosystem functioning (Grebmeier and Barry, 2007). They provide important services to the surrounding ecosystem and changes in these services may have large-scale impacts. Due to their complexity, the effects of climate change are supposed to be recognisable at an early stage in environments of such elevated productivity or diversity (Grebmeier et al., 2006a). Such a regime shift was observed in the Bering Sea, where the reduction of sea-ice cover translated into the rapid increase of pelagic fish and whale populations, and the simultaneous decrease of benthos production (Grebmeier et al., 2006a). However, Glover et al. (2010) have demonstrated that progressive change in a system can only be distinguished from stochastic change in long-term studies. Hotspot ecosystems might show too much natural variability to easily detect a change, and areas of lower overall process rate - coldspots - might provide a better indicator of change.

Benthic processes are coupled with the functioning of the entire marine system via biogeochemical cycles, and they are not only necessary to be understood in order to predict

global effects of climate change (Baretta et al., 1995; Ebenhöh et al., 1995), but also to protect areas essential for biogeochemical cycles in the face of increasing human activities. But data on benthic remineralisation in the Canadian Arctic is extremely scarce, and the lack of knowledge on the biodiversity-ecosystem function relationship in the Arctic does not allow estimating benthic function hotspots from diversity. Moreover, high temporal variability in food supply for the benthos interferes with regional comparisons, if the benthic remineralisation has not been measured in similar seasons.

It becomes evident that we need to investigate the influence of food supply and diversity including temporal and spatial scales on benthic remineralisation, before a valid long-term description of benthic ecosystem function hotspots in the Canadian Arctic can be made. Considering the different scales that are important for understanding changes in benthic ecosystem functioning, it is crucial to develop 'sentinel' sites that will allow us to monitor and compare variations and its causes.

4. GENERAL OBJECTIVE

The goal of this thesis is to provide a baseline for the understanding of benthic ecosystem functioning in soft-bottom environments of the Canadian Arctic, to find hotspots of high benthic ecosystem functions and to verify if these can be used as sentinel sites to monitor ecosystem changes, compared to sites of lower ecosystem functions - coldspots. For this, my work aims to determine how food availability, diversity and other environmental factors influence benthic remineralisation at different temporal and spatial scales at hotspots or coldspots (Fig. 4). Given the necessity to distinguish spatial from temporal variation for the estimation of the impact of future changes in relation to natural variability in a dynamic ecosystem such as the Arctic, my general objective is addressed in four major steps, which are presented in the following sections:

The objective of chapitre 1 is to verify, how seasonal variability affects benthic carbon remineralisation function. Specifically, I test the following hypotheses in the western Canadian Arctic: (1) The availability of food for benthic communities increases following the ice melt, (2) benthic biomass increases after the ice melt, (3) benthic carbon remineralisation increases following ice melt, and (4) spatial variability of benthic carbon remineralisation is determined by both food availability and benthic community patterns.

Chapitre 2 analyses how the description of spatial patterns is influenced by the single-flux or multiple-flux approach to benthic remineralisation function, and which environmental factors influence spatial variation in single and multiple benthic boundary fluxes. I address the following question and hypotheses: (1) What is the spatial variation of benthic boundary fluxes in the Beaufort Sea? The classical proxy of benthic activity, oxygen flux, does not describe overall spatial variation in fluxes. (3) A different combination of environmental conditions that vary either on a long-term (decadal) or short-term (seasonal to annual) scale determine each single flux. (4) A combination of environmental conditions varying on the short and long-term scale drive the overall spatial variation in benthic boundary fluxes.

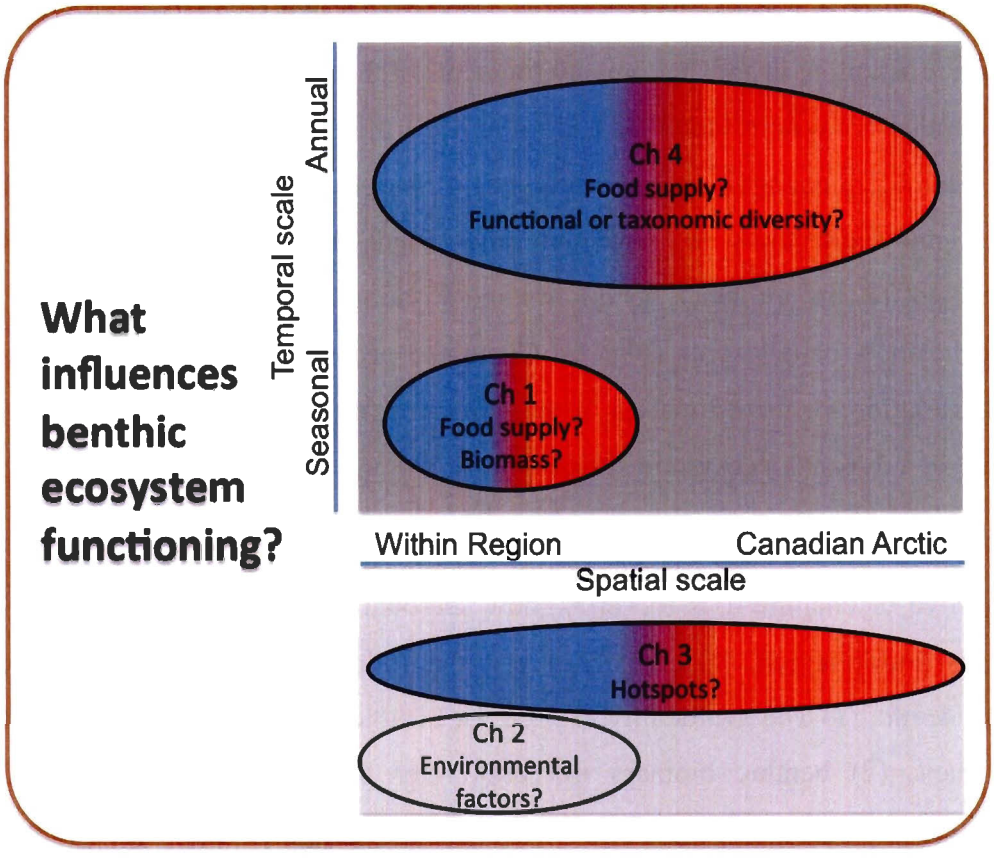

Fig. 4: Overview of how the four objectives analyse the different sources of variation in benthic ecosystem functioning (here: remineralisation) in this thesis. Bubbles represent which part of variation is treated in the respective chapter (Ch), and which driving factors were analysed. Coloured bubbles represent analyses of variation in hotspots *vs* coldspots (red vs blue, respectively). Note that spatial variation in benthic functioning was not always analysed across temporal scales.

Chapitre 3 gives an overview of present spatial patterns of multivariate benthic remineralisation function. The objective is to present (1) where the highest benthic fluxes are found, (2) where regions with high fluxes aresignificantly different from other regions within the Canadian Arctic, (3) whether benthic function hotspots are general hotspots (how the fluxes relate to other biological parameters) and (4) how benthic boundary fluxes can be used in ecological assessment.

Finally, chapitre 4 evaluates how interannual variation can affect our perception of changes in benthic ecosystem functions at hotspots or coldspots and the diversity-ecosystem function relation in dynamic systems such as the Arctic. Specifically, I test the following hypotheses: (1) Benthic remineralisation function is significantly different among years at hotspots but not at coldspots, (2) food availability for the benthos is significantly different among years at hotspots but not at coldspots, (3) Taxonomic community composition is not significantly different among years at hotspots or coldspots, (4) Functional community composition is not significantly different among years at hotspots or coldspots, and (5) Food supply explains temporal variation and macrofaunal community parameters explain spatial variation in benthic remineralisation function.

5. SAMPLING DESIGN

To obtain data that qualifies for analyses on different temporal and spatial scales, it was crucial to resample a same location (site) at different points in time. During the Circumpolar Flaw Lead Study (CFL; Deming and Fortier, 2011) in 2008, the ArcticNet-CHONe (Canadian Healthy Oceans Network; Snelgrove et al., 2012) expeditions in 2008 and 2009 and the Malina expedition in 2009 I sampled a total of 47 stations for the major parameters of benthic remineralisation (ship-board microcosm incubations) and sediment pigment concentration (Fig. 5, Table 1).

Additional benthic parameters could be sampled at different subsets of the 47 stations, and 14 sites were sampled more than once (Table 1). According to my objectives, sampling and data analyses was conducted for:

Chapitre 1. Seasonal patterns: 5 sites in spring and summer each (benthic carbon remineralisation, sediment pigment concentration, benthic biomass; Amundsen Gulf; CFL)

Chapitre 2. Habitat influence and spatial patterns: 8 sites in summer (benthic oxygen flux and nutrient remineralisation, sediment pigment concentration, sediment and habitat properties; Mackenzie Shelf and Slope; Malina)

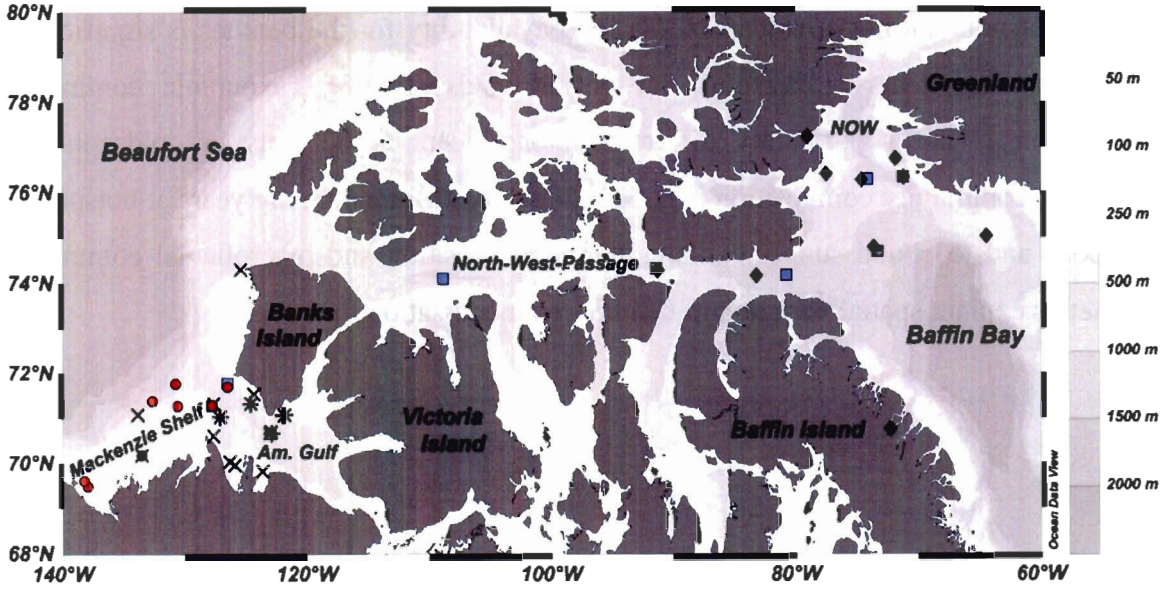

Fig. 5: Station map of this thesis. Symbols represent sites sampled during different expeditions in the Canadian Arctic in 2008 and 2009. +: CFL spring; x: CFL summer/fall; ◆: ArcticNet-CHONe 2008; ○: Malina; ■ArcticNet-CHONe 2009. NOW = North Water Polynya; Am. Gulf = Amundsen Gulf. Note that symbols can overly each other if sampling at the same location in different expeditions was achieved

Chapitre 3. Hotspot spatial patterns: 42 sites between summer and fall (benthic oxygen flux and nutrient remineralisation; entire study area; all expeditions)

Chapitre 4. Interannual patterns: 9 sites in summer and fall each (benthic oxygen flux and nutrient remineralisation, sediment pigment concentration, benthic diversity; subset in entire study area; all expeditions).

Table 1 provides an overview of the origin of the data, and more information on the precise methods can be found in the respective chapters.

Table 1: Station list. Sites, their original expedition label ('Station'), sampling date, region, bottom water depth, geographic position, the according symbol in Fig. 5, obtained data and the presentation in the following chapitres ('Ch') are presented. Obtained data: B = biomass; D = macrofaunal diversity; G = geochemical sediment properties; N = benthic nutrient fluxes; O = benthic oxygen flux; P = sediment pigment concentration

Site	Station	Date	Region	Depth	Latitude (°N)	Longitude (°W)	Symbol	Data	Ch 1	Ch 2	Ch 3	Ch 4
D 34	D35	2008-04-02	AG	215	71.069	121.944	+	OPB	✔			
	D34	2008-05-24	AG	185	71.076	121.811	+	OPB	✔			
	D34	2008-07-13	AG	186	71.070	121.823	x	ONPB	✔		✔	
D 37	D37	2008-04-10	AG	245	71.312	124.603	+	OPB	✔			
	2011-10A	2008-08-02	AG	251	71.318	124.595	x	ONPB	✔		✔	
1020A	1020A	2008-05-06	AG	255	71.029	127.088	+	OPB	✔			
	1020A	2008-07-27	AG	245	71.028	127.088	x	ONPB	✔		✔	
405	405	2008-05-19	AG	505	70.662	122.887	+	OPB	✔			
	405B	2008-06-10	AG	546	70.667	123.010	x	ONPB	✔		✔	
	405-10A	2008-07-21	AG	596	70.707	122.939	x	ONPD	✔		✔	✔
	405	2009-10-16	AG	559	70.665	122.996	■	ONPD			✔	✔
FB	1116	2008-06-14	AG	230	70.042	126.277	x	ONPB	✔		✔	
	FB3	2008-06-16	AG	97	69.968	125.862	x	ONPB	✔		✔	
DB	DB01	2008-06-19	AG	95	69.827	123.604	x	ONP			✔	
1216	1216	2008-06-23	AG	151	70.615	127.616	x	ONP			✔	
1200	1200	2008-06-27	AG	207	71.532	124.297	x	ONP			✔	
9002	9002	2008-07-07	MS	219	74.298	125.376	x	ONP			✔	
408	408-10A	2008-07-25	AG	206	71.323	127.606	x	ONPD			✔	✔
	140	2009-08-07	AG	154	71.285	127.783	O	ONPDG		✔	✔	✔
	408	2009-10-13	AG	152	71.286	127.782	■	ONP			✔	
437	110	2009-08-06	AG	400	71.696	126.477	O	ONPG		✔	✔	
	437	2009-10-14	AG	320	71.779	126.477	■	ONP			✔	
308	308	2009-10-19	VMS	541	74.101	108.836	■	ONP			✔	
434	434	2008-06-30	MD	45	70.177	133.537	x	ONPD			✔	✔
	390	2009-07-31	MD	47	70.178	133.569	O	ONPDG		✔	✔	✔
435	435	2008-07-02	MS	318	71.072	133.876	x	ONPD			✔	✔
	345	2009-08-16	MS	577	71.382	132.652	O	ONPDG		✔	✔	✔

Table 1 continued

Site	Station	Date	Region	Depth	Latitude (°N)	Longitude (°W)	Symbol	Data	Ch 1	Ch 2	Ch 3	Ch 4
690	690	2009-08-01	MD	55	69.486	137.942	○	ONPG		✔	✔	
260	260	2009-08-04	MS	60	71.269	130.613	○	ONPG		✔	✔	
680	680	2009-08-10	MD	125	69.611	138.235	○	ONPG		✔	✔	
235	235	2009-08-22	MS	576	71.764	130.766	○	ONPG		✔	✔	
304	Barrow Strait	2008-09-06	LS	353	74.271	91.248	◆	ONPD			✔	✔
	304	2009-10-23	LS	331	74.318	91.406	■	ONPD			✔	✔
301	301	2008-09-08	LS	707	74.153	83.209	◆	ONPD			✔	✔
	323	2009-10-25	LS	786	74.172	80.726	■	ONPD			✔	✔
101	101	2008-09-15	NOW	402	76.401	77.492	◆	ONP			✔	
108	108	2008-09-14	NOW	444	76.270	74.594	◆	ONPD			✔	✔
	109	2009-10-28	NOW	451	76.290	74.137	■	ONPD			✔	✔
115	115	2008-09-13	NOW	668	76.326	71.215	◆	ONPD			✔	✔
	115	2009-10-29	NOW	669	76.335	71.238	■	ONPD			✔	✔
205	205	2008-09-17	NOW	623	77.219	78.981	◆	ONP			✔	
126	126	2008-09-18	NOW	323	77.343	73.441	◆	ONP			✔	
233	233	2008-09-20	NOW	696	76.739	71.844	◆	ONP			✔	
136	136	2008-09-10	BB	795	74.786	73.633	◆	ONPD			✔	✔
	136	2009-10-30	NOW	810	74.687	73.349	■	ONPD			✔	✔
140	140	2008-09-11	BB	286	75.028	64.477	◆	ONP			✔	
GF	Gibbs fjord 2	2008-09-24	GF	452	70.768	72.264	◆	ONP			✔	

CHAPITRE 1
SPRING-TO-SUMMER CHANGES AND REGIONAL VARIABILITY OF BENTHIC PROCESSES IN THE WESTERN CANADIAN ARCTIC

RÉSUMÉ DU PREMIER ARTICLE

Seasonal dynamics in the activity of Arctic shelf benthos have been the subject of few local studies, and the pronounced among-site variability characterizing their results makes it difficult to upscale and generalize their conclusions. In a regional study encompassing five sites at 100-595 m water depth in the southeastern Beaufort Sea, we found that total pigment concentrations in surficial sediments, used as proxies of general food supply to the benthos, rose significantly after the transition from ice-covered conditions in spring (March–June 2008) to open-water conditions in summer (June–August 2008), whereas sediment Chl *a* concentrations, typical markers of fresh food input, did not. Macrobenthic biomass (including agglutinated foraminifera > 500 μm) varied significantly among sites (1.2–6.4 g C m^{-2} in spring, 1.1–12.6 g C m^{-2} in summer), whereas a general spring-to-summer increase was not detected. Benthic carbon remineralisation also ranged significantly among sites (11.9–33.2 mg C m^{-2} d^{-1} in spring, 11.6–44.4 mg C m^{-2} d^{-1} in summer) and did in addition exhibit a general significant increase from spring to summer. Multiple regression analysis suggests that in both spring and summer, sediment Chl *a* concentration is the prime determinant of benthic carbon remineralisation, but other factors have a significant secondary influence, such as foraminiferan biomass (negative in both seasons), water depth (in spring) and infaunal biomass (in summer). Our findings indicate the importance of the combined and dynamic effects of food supply and benthic community

patterns on the carbon remineralisation of the polar shelf benthos in seasonally ice-covered seas.

Keywords: Arctic, Beaufort Sea, Pelagic-benthic coupling, Seasonality, Carbon remineralisation, Benthic biomass

This first publication was co-authored by myself, Prof. Philippe Archambault, my colleagues Dr. Tobias Tamelander and Dr. Paul E. Renaud and by Prof. Dieter Piepenburg. It has been accepted in its final version and published by the editors of the journal *Polar Biology* in 2011. As first author, I conducted most of the experimental work, the laboratory and statistical analyses and wrote the publication. Prof. Dieter Piepenburg and Prof. Philippe Archambault designed the original idea and contributed to statistical analyses and writing. Prof. Dieter Piepenburg and Dr. Tobias Tamelander also participated in experimental work, and the latter and Dr. Paul E. Renaud contributed to the writing. Parts and short versions of this publication were presented at the following conferences: (1) *Arctic Change* in Québec (Canada) in December 2008 (2) *Arctic Frontiers* in Tromsø (Norway) in January 2009 (3) *CFL-All-Hands-Meeting* in Winnipeg (Canada) in November 2009.

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SPRING-TO-SUMMER CHANGES AND REGIONAL VARIABILITY OF BENTHIC PROCESSES IN THE WESTERN CANADIAN ARCTIC

Introduction

Biological processes in the Arctic are known to exhibit a pronounced seasonality with ice cover being one of the major underlying mechanisms (Carmack and Wassmann, 2006). Following the ice melt during the spring-to-summer transition, the mismatch between peak primary production and zooplankton grazing allows for an enhanced export of organic material to the seafloor (Wassmann et al., 2006). This provides an important food input to benthic communities, and several studies have described the significant increase in benthic activity in response to an organic matter pulse for the oceans in general (Graf, 1992; Pfannkuche, 1993) and for Arctic regions in particular (Renaud et al., 2007b; Rysgaard et al., 1998). The remineralisation of organic matter at the seafloor is a source of nutrient release to the water column (Grebmeier et al., 2006a) and a significant pathway in the global carbon budget (Klages et al., 2004).

Strong pelagic-benthic coupling has been widely suggested as a general feature of Arctic shelves (Ambrose and Renaud, 1995; Grebmeier and Barry, 1991; Piepenburg et al., 1997; Wassmann et al., 2006), in terms of both quantity and quality of the organic matter exported from the water column and/or sea ice to the seabed (Morata et al., 2008). During the Shelf-Basin Interaction Study (SBI) in the Chukchi Sea, vertical export and benthic response were measured in spring and summer in 2002 and 2004 (Lepore et al., 2007). In 2002, the export of particulate organic carbon (POC) was much higher in summer than in spring and coincided with an, albeit less pronounced, increase in benthic respiration (Moran et al., 2005). In 2004, however, POC export and benthic carbon respiration were only slightly less under ice cover than in summer open-water conditions (Lalande et al., 2007; Lepore et al., 2007). The findings – elevated chlorophyll *a* (Chl *a*) concentrations under ice (Lalande et al., 2007), more than twice as high absolute export rates but only slightly higher benthic respiration – suggest that there was a distinct spring bloom but lateral advection of

organic matter into the central Arctic Ocean, which resulted in a lack of a seasonal benthic activity boost (Lepore et al., 2007). Enhanced benthic respiration has been related to higher nutritive quality of the phytodetritus reaching the seabed (Morata and Renaud, 2008; Sun et al., 2009). In the Barents Sea, a sharp increase in benthic activity was related to the supply of fresh food, as indicated by high Chl *a* export and high sediment pigment concentrations (Renaud et al., 2008). In the southeastern Beaufort Sea, spring-to-summer dynamics have been studied at one time-series site in Franklin Bay (Amundsen Gulf) during the Canadian Arctic Shelf Exchange Study (CASES) in 2004. A seasonal increase in benthic carbon remineralisation was recorded (Renaud et al., 2007b), whereas an increase in the availability of fresh food at the sea floor could only be confirmed after pigment analyses with a higher resolution (Morata et al., 2010). A considerable increase in benthic respiration from spring to summer has also been reported from the North Water Polynya (NOW), where carbon remineralisation was driven by micro- and meiobenthic communities in spring and by macrobenthic communities in summer (Grant et al., 2002). The composition of the benthic community also plays a major role in determining benthic carbon remineralisation in Arctic environments (Clough et al., 2005), as documented in experimental studies (MacMahon et al., 2006). However, much less is known about seasonal changes of the structure and activity of benthic communities in relation to dynamics of food availability (Renaud et al., 2008; Witman et al., 2008).

The reduction in Arctic sea ice in response to climate change and ocean warming is well documented (Barber et al., 2009), but its effects on biological processes are hard to predict (ACIA, 2004; Smetacek and Nicol, 2005). Wassmann et al. (2011) highlighted that climate change has already resulted in clearly discernable changes in marine Arctic ecosystems, but the number of well-documented changes in planktonic and benthic systems was surprisingly low. Although total primary production in the Arctic Ocean will likely increase (Arrigo et al., 2008), its reduced seasonal variability and increased pelagic remineralisation might result in a general decrease of the vertical flux of fresh organic matter to the bottom (Forest et al., 2010; Forest et al., 2011; Piepenburg, 2005). There is still controversy about the actual scope and direction of future changes in primary

production and vertical flux patterns (Wassmann et al., 2008). Regardless, shifts in benthic community metabolism and composition are expected (ACIA, 2004; Archambault et al., 2010; Carroll et al., 2008; Grebmeier et al., 2006a; Sun et al., 2009) and are likely to influence the ecosystem at higher trophic levels (Bluhm and Gradinger, 2008). Our incomplete knowledge about spring-to-summer dynamics of benthic processes makes it difficult to reliably predict their response to climate-induced changes in the abiotic environment and to concurrent changes in the timing and magnitude of primary production, the quality of organic material deposited on the seafloor, and the composition of benthic communities. For this purpose, it is crucial to assess the relationships among seasonal dynamics in food supply, benthic standing stock and benthic carbon remineralisation on a regional scale.

The objective of this study was to describe how seasonal changes in the availability of food influence benthic carbon remineralisation – the rate of carbon cycling – in the southeastern Beaufort Sea. Since ice cover is a major seasonal characteristic of polar regions, differences between the ice-covered period (spring) and subsequent open-water period (summer) were studied. Our hypotheses were that (1) the availability of food for benthic communities increases significantly following the ice melt, (2) benthic biomass increases after the ice melt, (3) benthic carbon remineralisation increases significantly following ice melt, and (4) spatial variability of benthic carbon remineralisation is determined by both food availability and benthic community patterns, here tested as biomass.

Materials and methods

Study Region

This study was conducted in the southeastern Beaufort Sea with emphasis on the Amundsen Gulf, including Franklin Bay (Fig. 1.1). The area is usually covered by sea ice

from November to June (Galley et al., 2008). In 2008, it was generally covered by sea ice until mid-May (Barber et al., 2010; NSIDC, 2010). Primary production ranges from 30-70 g C m^{-2} $year^{-1}$, indicating generally oligotrophic conditions (Sakshaug, 2004). In the Cape Bathurst Polynya, rates are higher, reaching 90-175 g C m^{-2} $year^{-1}$ (Arrigo and van Dijken, 2004). Intensive blooms related to ice-edge upwelling events were documented for coastal regions of the Amundsen Gulf, including Franklin Bay, in June 2008 (Mundy et al., 2009; Tremblay, pers. comm.). The study area is dominated by coastal shelves with maximum depths of 600 m in the center of the Amundsen Gulf. Seafloor sediments are usually fine, composed of more than 70% silt and clay (Conlan et al., 2008). Sediment characteristics indicate that marine material dominated the flux in summer and is more degraded in the Amundsen Gulf, whereas on the Mackenzie Shelf material of terrestrial origin is abundant in fall (Magen et al., 2010; Morata et al., 2008). Sediment Chl *a* concentrations are reported to be low (0-2 mg m^{-2} in the Amundsen Gulf and 3 to 4 mg m^{-2} in Franklin Bay), with Chl *a*-to-phaeopigment ratios not exceeding 0.2 in summer and fall (Morata et al., 2008). In 2004, accessory sediment pigments consisted mostly of fucoxanthin in the western Amundsen Gulf and of Chl *b* in the eastern part (Morata et al., 2008). Sediment pigment concentrations in spring have only been reported for Franklin Bay, where concentrations were similar to those encountered in summer (Renaud et al., 2007a).

Environmental Conditions

Near-bottom water temperature and salinity were determined by the shipboard CTD probe at each station 10 m above the seafloor. We used sea ice concentration maps available from the CERSAT Ifremer group (http://cersat.ifremer.fr/fr/data/discovery/by_parameter/sea_ice/psi_ssmi) based on the daily brightness temperature maps from the National Snow and Ice Data Centre (Maslanik and Stroeve, 1990), which are acquired from the special sensor microwave imager (SSM/I) onboard the DMSP satellite to extract sea ice concentration data. Daily sea ice concentration data were extracted for each station between March and August 2008. The average of daily concentration for the 14 days preceding the sampling date was used to

determine the ice cover for each station. Ice break-up in the region typically takes 1-2 weeks (Galley et al., 2008). We considered the period of 14 days long enough to assure that ice cover was not incidental (e.g. being due to a passing ice floe) and short enough to assure that it describes the ice condition that should be timely linked to benthic processes.

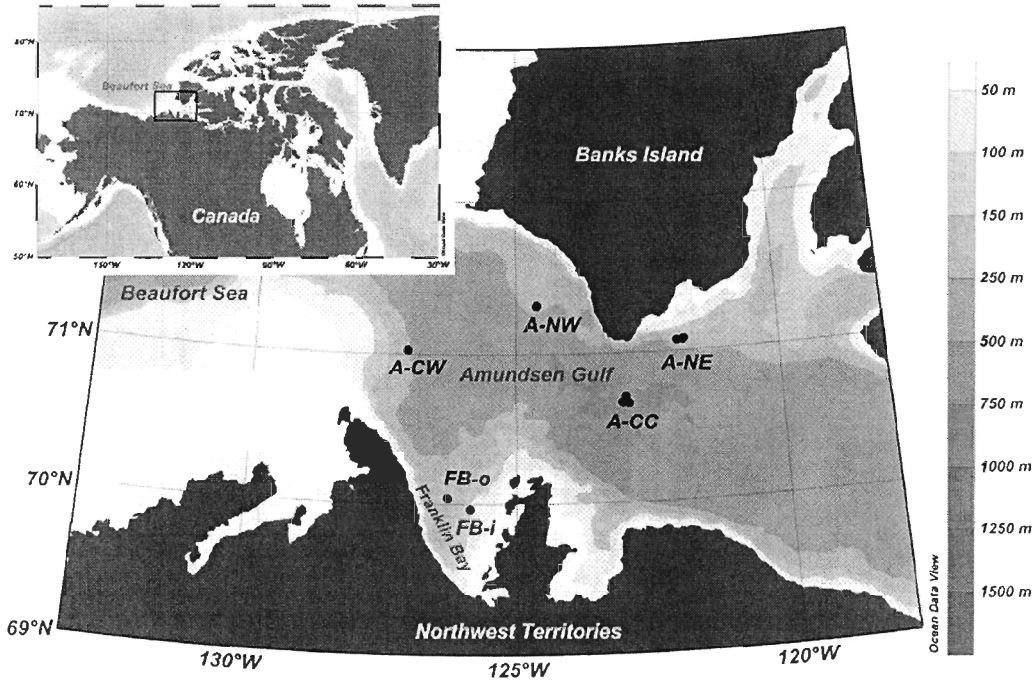

Fig. 1.1: Locations of sites sampled for benthic processes during ice-covered (spring) and open-water (summer) conditions in 2008. A = Amundsen Gulf, FB = Franklin Bay; C, E, N, W = central, east, north, west; i = ice-covered, o = open water. Note that one point on the map can represent two sampling events when exact relocation in summer was achieved

Table 1.1: Sampled stations, environmental conditions, temporal factor (season) and number of replicates used to determine sediment oxygen demand (SOD), chlorophyll *a* concentrations in the sediment (Chl *a*) and macrobenthic infauna biomass (Biomass). Daily ice cover concentrations averaged over the 14 days preceding the date of sampling was used to determine sea ice cover [%]. . A = Amundsen Gulf, FB = Franklin Bay; C, E, N, W = central, east, north, west; CFL = Circumpolar Flaw Lead System Study

Station	CFL Station Label	Date	Water Depth [m]	Position				Sea ice cover [%]	Sal_{bot}	T_{bot} [°C]	Season	SOD (n)	Chl *a* (n)	Biomass (n)
				Latitude		Longitude								
A-NE-i	D 34	24/Mar/08	185	71.076	N	121.811	W	100	34.5	-0.1	ice	5	3	5
A-NE-i-2	D 35	02/Apr/08	215	71.069	N	121.944	W	98	34.5	-0.1	ice	5	3	5
A-NE-o	D 34	13/Jul/08	185	71.07	N	121.823	W	0	34.3	-0.6	open	5	3	3
A-NW-i	D 37	10/Apr/08	245	71.312	N	124.603	W	95	34.6	-0.1	ice	5	3	5
A-NW-o	D 37	02/Aug/08	250	71.318	N	124.595	W	0	34.5	-0.2	open	5	3	5
A-CW-i	1020A	06/May/08	255	71.029	N	127.088	W	90	33.1		ice	5	3	5
A-CW-o	1020A	27/Jul/08	245	71.028	N	127.088	W	0	n/a	-0.1	open	5	3	5
A-CC-i	405	19/May/08	505	70.662	N	122.887	W	60	34.5		ice	4	3	5
A-CC-o	405B	10/Jun/08	545	70.667	N	123.01	W	11	34.8	0.4	open	5	3	5
A-CC-o-2	405B	21/Jul/08	595	70.707	N	122.939	W	0	34.8	0.4	open	5	3	n/d
FB-i	FB03	16/Jun/08	100	69.968	N	125.862	W	34*	33.4	-1.3	ice*	5	3	5
FB-o	1116	14/Jun/08	230	70.042	N	126.277	W	22	33.3	-1.3	open	5	3	5

* Station was located in fast ice, while general ice cover had retreated

Field Sampling

Samples were collected at five sites ranging in water depth from 100 to 595 m at least once in each season (ice-covered and open-water condition) between March and August 2008 onboard the icebreaker CCGS Amundsen (Table 1.1). Ice conditions for the Amundsen Gulf have been classified as 'ice covered' with ≥80% ice cover, 'open' with ≤20% ice cover (Galley et al., 2008; Hammill, 1987) and as ice 'break-up' with ≤80% and ≥20% ice cover (Galley et al., 2008). Adopting this approach, we considered a station to be 'ice-covered' if the 14-day average sea ice concentration was above 80% and 'open' if average sea ice concentration was below 20%. Fifty percent ice cover represents the average ice concentration of 'break-up' condition and implies that a site was closer to 'ice-covered' than 'open' for at least 7 days before sampling. We verified ice concentration of all sites in break-up condition with weekly ice charts for the western Canadian Arctic published by the Canadian Ice Service (CIS) available on http://www.ec.gc.ca/glaces-ice/. Sites were located in the Amundsen Gulf (A-CC, A-CW, A-NE, A-NW) and Franklin Bay (FB) (Fig. 1.1). In Franklin Bay, sampling was conducted at two distinct sites within 2 days: FB-o was located where the ice edge had retreated for more than 10 days at 18 km distance from FB-i, which was located at the ice edge (Table 1.1). At each sampling event ('station'), an USNEL box corer was deployed for collecting seafloor sediments. From each box core, five sub-cores of 11 cm diameter and 20 cm sediment depth were taken for assessing benthic carbon remineralisation in microcosm incubations and three additional sub-cores of 5 cm diameter and 10 cm length were taken for determining sediment properties (Table 1.1).

Sediment Pigment Concentration

Samples from the sediment surface (0 to 1 cm) of additional sub-cores were frozen immediately at –20 °C for later pigment analysis. Chl *a* and phaeopigment concentrations were analysed fluorometrically following a modified version of the protocol by Riaux-Gobin and Klein (1993). Two grams of wet substrate were incubated with 10 ml 90% Acetone (v/v) for 24 h at 4 °C, and the supernatant was measured in a Turner Design 20

fluorometer before and after acidification. Chl *a* and total pigment concentration (Chl *a* + phaeopigments) were determined and used in statistical analyses. Quantities are expressed as microgram pigment per gram of dry sediment [$\mu g\ g^{-1}$].

Benthic Carbon Remineralisation

Incubations of sediment microcosms were run in a dark, temperature-controlled room (2 to 4 °C) for 24 to 48 h. Prior to the onset of measurements, sediment cores were carefully topped with bottom water collected by the rosette at the same site and then allowed to acclimate for 6-8 h while being saturated with oxygen to avoid suboxic conditions during the experiment. At the onset of measurements, the microcosms were hermetically closed and bubbles were removed. During the incubation, the water overlying the sediment was constantly stirred without resuspending the sediment surface. Total sediment oxygen demand (SOD) was determined as the decrease in oxygen concentrations in the water phase and was measured periodically (4-8 h intervals) with a non-invasive optical probe (Fibox 3 LCD, PreSens, Regensburg, Germany), until it had declined by approximately 20%. Three additional incubation cores containing bottom water only acted as controls for assessing the oxygen uptake due to processes within the water column. SOD values were determined as the slope of the linear regression of oxygen concentration in sediment microcosms on incubation time. Average oxygen decrease rates from the three control cores were subtracted, and benthic carbon remineralisation values (mg C $m^{-2} d^{-1}$) were calculated from SOD rates using a respiration coefficient of 0.8 (Brey, 2001).

Macrobenthic biomass

Each sediment microcosm was sieved through a 0.5 mm mesh under running sea water at the end of incubations to determine biomass of macrofaunal communities. The sieve residue was preserved in a buffered 4% seawater-formaldehyde solution and analysed for species composition and abundance under a stereomicroscope in the lab. Metazoan infauna biomass was estimated by determining the formaldehyde wet weight (except at station A-CC-o2 see Table 1.1) and applying taxon-specific wet weight to carbon conversion factors (Brey et al., 2010). All macrofaunal foraminifera except for five

individuals were agglutinated forms. For sorting, we used the method described by Moodley et al. (2002) based on the presence of cytoplasma and appearance of shells. Biomass of macrofaunal foraminifera was estimated from abundance figures using an average value of 5 μg C individual^{-1} (Altenbach, 1985). Abundance of foraminifera at station A-CW-i could not be analysed, as the remains of this sample were discarded after macrofauna sorting. There is good evidence, however, that at this site the foraminiferan biomass was lower in spring than in summer, since no foraminifera were detected by visual inspection of the spring sieve residues, whereas in summer, tests were easily visible although abundances were lower than in all other samples. Total benthic biomass was computed by adding foraminiferan and infaunal biomass values, assuming 0 for the three stations where foraminiferan data were lacking. For statistical analysis, foraminifera data were assigned ranks in steps of 50 mg C m^{-2}. This interval allowed for capturing within-station variances and at the same time to assign the lowest rank to replicates at stations from which no data were available.

Data Analysis

One-way ANOVA was used to test seasonal differences in salinity and temperature (two levels: ice, open). Earlier studies have provided evidence that variance among sub-cores from the same box core is not significantly smaller than variance among different box cores taken at the same station (Renaud et al., 2007a). Sub-cores were, therefore, treated as true replicates in statistical analyses. An orthogonal two-way ANOVA was used to test the differences between 'seasons' (two levels: ice, open), 'sites' (five levels: A-CC, A-CW, A-NE, A-NW, FB) and their interactions in sediment Chl *a* concentration, total sediment pigment concentration, benthic biomass and carbon remineralisation. Tukey's post-hoc tests were applied to identify differences when a source of variation was significant. Prior to ANOVA, normality was verified using Shapiro-Wilk's test and homogeneity of variances was verified using Levene's test and visual analysis of residuals. Data were transformed using natural logarithm if variances were not homogeneous. To identify the drivers of benthic carbon remineralisation in spring and summer (separately), Mallow's C*p* (MC*p*) and adjusted R^2 were used to determine the best-subset linear multiple regression

model. MC*p* compares a given reduced model to the full model, and a smaller statistic indicates a better model (Quinn and Keough, 2002). Water depth, sediment Chl *a* concentration, total sediment pigment concentration, infaunal biomass and ranked foraminiferan biomass were predicting variables of the full model. We tested for collinearity of variables retained in the best-subset model using the variance inflation factor (VIF). When VIF is > 10, collinearity is assumed critical (Quinn and Keough, 2002). This was not the case for either of the best-subset models.

Results

Temporal Dynamics from spring to summer

Environmental conditions

Near-bottom water temperature at the study sites varied between –1.3 to 0.4 °C, and near-bottom salinity ranged between 33.1 and 34.8, as determined by the shipboard CTD probe 10 m above the seafloor (Table 1.1). The greatest difference was a decrease in temperature of 0.5 °C (from –0.1 to –0.6 °C) at site A-NE from March to July (Table 1.1). However, neither temperatures nor salinities differed significantly between spring and summer (one-way ANOVA, salinity $F_{1,\ 7} = 0.23$, $P = 0.64$; temperature $F_{1,\ 7} = 0.44$, $P = 0.53$). Average sea ice cover during the 14 days before sampling at a given site varied from 100 to 60% between March and May and from 34 to 0% between June and August (Table 1.1). The higher ice cover in June (34 and 22%) was measured in Franklin Bay, where sampling was conducted at a distance of 18 km (FB-o) and < 0.5 km (FB-i) to a visible ice edge. CIS ice charts showed that sites A-CC and FB were completely ice-covered at least seven of 14 days prior to sampling on May 19th and June 16th, respectively. Based on these results, stations were grouped into ice-covered (or spring) stations when ice cover was ≥34% and into open-water (or summer) stations when ice cover was ≤22%.

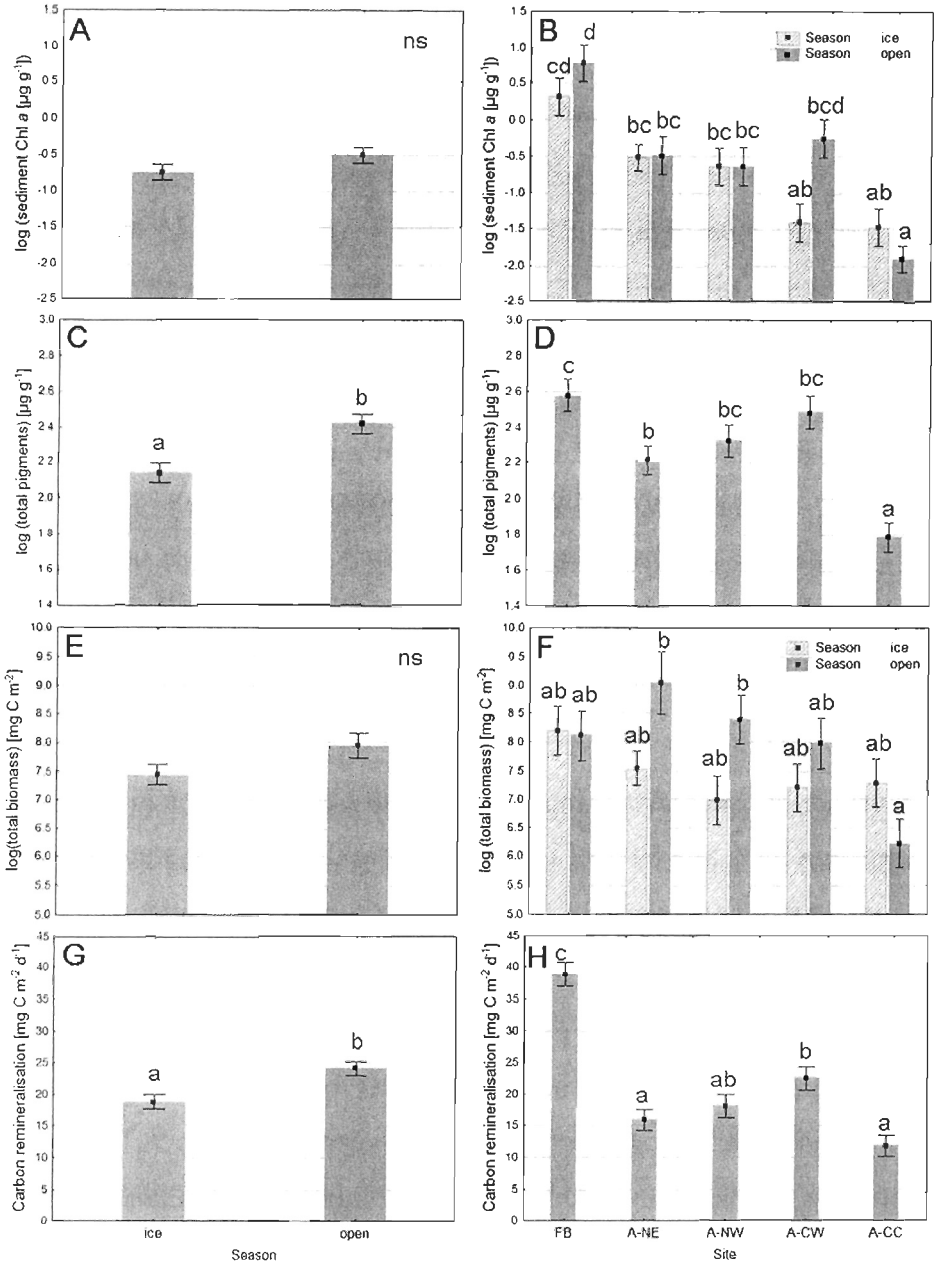

Fig. 1.2: Seasonal and spatial patterns in benthic processes in the southeastern Beaufort Sea in 2008. Differences in Season (A, C, E, G), Site (D, H) and significant interactions between Season and Site (B, F) in sediment Chl *a* concentration (A, B) sediment pigment concentration (C, D), benthic biomass (E, F), and benthic carbon remineralisation (G, H) following univariate orthogonal two-way ANOVA are presented. Means ± SE. Lower case letters indicate significantly different groups identified using Tukey's post-hoc testing, ns = not significant. A = Amundsen Gulf, FB = Franklin Bay; C, E, N, W = central, east, north, west; i = ice-covered, o = open water

Sediment pigment concentration

Chl *a* concentrations in the surficial seafloor sediments varied between 0.24 and 1.36 μg g^{-1} under ice cover and between 0.15 and 2.39 μg g^{-1} in open-water conditions (Table 1.2). There was a significant interaction between site and season ($F_{4,26} = 3.09$, $P = 0.03$; Fig. 1.2A, B). Phaeopigment concentrations ranged from 5.05 to 9.93 μg g^{-1} and from 6.23 to 14.61 μg g^{-1}, respectively. They increased at all sites from spring to summer (Table 1.2). Total sediment pigment concentrations varied from 5.29 to 10.51 μg g^{-1} under ice cover and from 6.39 to 17.00 μg g^{-1} in open water. The values were significantly different between seasons ($F_{1,26} = 13.19$, $P < 0.01$) and among sites ($F_{4,26}$= 13.57, $P < 0.001$; Fig. 1.2 C, D). No interaction between season and site was observed ($F_{4,26}$ = 0.52, P = 0.72). Four site groups were identified using Tukey's post-hoc test with A-CC having a significantly lower sediment pigment concentration than all other sites. Highest pigment concentrations were found at FB.

Benthic biomass

Macrofauna in the sediment samples was mostly composed of infaunal polychaetes contributing between 33% and 84% of total biomass at the different stations (unpub. data). Macrobenthic infauna biomass varied from 916 to 6166 mg C m^{-2} under ice cover and from 900 to 12566 mg C m^{-2} in open water (Table 1.2). At some sites, large agglutinated foraminifera (test sizes > 500 μm) were particularly abundant, with biomass values ranging from undetermined to 592 mg C m^{-2} under ice cover conditions and undetermined to 662 mg C m^{-2} in open water. They accounted for between << 1 % to > 10 % of the total macrobenthic biomass (Table 1.2). Total macrobenthic biomass (infauna and foraminifera) reached values from 1230 to 6398 mg C m^{-2} under ice cover and from 1055 to 12649 mg C m^{-2} in open-water conditions. There was a significant interaction between site and season ($F_{4,43} = 3.17$, $P = 0.02$; Fig. 1.2 E, F), and three groups were identified following Tukey's post-hoc test.

Table 1.2: Carbon remineralisation, sediment parameters and macrobenthic biomass at each location (A = Amundsen Gulf, FB = Franklin Bay; C, E, N, W = central, east, north, west) and season. Within-station averages ± SE. Chl *a* = chlorophyll *a* concentration, Phaeo = phaeopigment concentration; Foram = foraminifera > 500 μm; n/d = not determined

Location	Season	Chl *a* [$\mu g\ g^{-1}$]	Phaeo [$\mu g\ g^{-1}$]	Infauna [mg C m^{-2}]	Foram [mg C m^{-2}]	Carbon remineralisation [mg C $m^{-2}\ d^{-1}$]
A-NE	ice	0.72 ± 0.18	6.80 ± 0.54	2526 ± 881	237 ± 32	16.7 ± 2.9
	ice	0.55 ± 0.08	8.53 ± 0.37	1138 ± 186	n/d	13.0 ± 2.6
	open	0.74 ± 0.32	10.83 ± 3.97	8382 ± 2366	662 ± 140	16.9 ± 1.9
A-NW	ice	0.54 ± 0.06	9.02 ± 0.51	1102 ± 246	128 ± 36	12.7 ± 0.6
	open	0.53 ± 0.02	10.39 ± 0.51	12566 ± 9012	83 ± 11	23.4 ± 4.5
A-CW	ice	0.31 ± 0.15	9.93 ± 1.09	2919 ± 1712	n/d	20.8 ± 2.0
	open	0.80 ± 0.15	13.45 ± 0.73	3912 ± 1320	36 ± 6	24.2 ± 1.5
A-CC	ice	0.24 ± 0.05	5.05 ± 0.35	916 ± 168	592 ± 22	11.9 ± 2.2
	open	0.16 ± 0.02	6.23 ± 0.66	900 ± 723	155 ± 7	11.6 ± 3.1
	open	0.15 ± 0.04	7.08 ± 0.28	n/d	n/d	11.9 ± 1.8
FB	ice	1.36 ± 0.12	9.14 ± 1.00	6166 ± 3513	232 ± 23	33.2 ± 2.4
	open	2.39 ± 0.79	14.61 ± 1.40	3600 ± 719	5 ± 2	44.4 ± 4.0

Benthic carbon remineralisation

Carbon remineralisation by the sediment community ranged from 11.9 mg C $m^{-2}\ d^{-1}$ to 33.2 mg C $m^{-2}\ d^{-1}$ in spring under ice cover and from 11.6 mg C $m^{-2}\ d^{-1}$ to 44.4 mg C $m^{-2}\ d^{-1}$ under open water in summer (Table 1.2). The values varied significantly between seasons ($F_{1,\ 49} = 11.34$, $P < 0.001$) and among sites ($F_{4,\ 49} = 33.37$, $P < 0.001$) (Fig. 1.2 G, H). Following Tukey's Post-hoc test, four groups were identified with only FB showing higher carbon remineralisation than all other sites (Fig. 1.2 H). Remineralisation was lowest at A-CC. No interaction between season and site was observed ($F_{4,49} = 2.12$, $P = 0.09$).

Table 1.3: Adjusted R^2 and standardized regression coefficients of benthic parameters (Depth – water depth, Infauna – biomass of infaunal macrobenthos, Foram = biomass of foraminifera > 500 μm, Chl *a* – sediment chlorophyll *a* concentration, Pigments = total sediment pigment concentration) predicting benthic carbon remineralisation in the two different seasons (ice-covered spring, open–water summer). Whole model results are presented for the best-subset solution following MC*p* criteria (Effects – number of parameters included in the model). Absence of standardized regression coefficients indicate the parameters were not retained in the model

Season	Adjusted R^2	*F*	*P*	Depth	Infauna	Chl *a*	Pigments	Foram	MC*p*	Effects
Ice	**0.57**	**13.42**	**<0.001**	**0.35**		**1.02**		**-0.43**	**4.88**	**3**
	0.58			0.34	0.18	0.94		-0.4	5.15	4
	0.55					0.74		-0.31	5.19	2
	0.56				0.18	0.66		-0.28	5.39	3
	0.59			0.52	0.2	0.94	0.27	-0.29	6	5
Open	**0.74**	**22.07**	**<0.001**		**0.25**	**0.63**		**-0.23**	**2.89**	**3**
	0.71				0.21	0.77			3.97	2
	0.74				0.33	0.81	-0.27	-0.3	4.12	4
	0.73			0.11	0.32	0.67		-0.23	4.54	4
	0.68					0.84			5.19	1

Drivers of spatial variability of benthic carbon remineralisation in spring and summer

MC*p* criteria and adjusted R^2 identified the best-subset regression model for ice-covered conditions in spring with depth, Chl *a* concentration and foraminiferan biomass retained as predictive variables (Table 1.3). Benthic carbon remineralisation was positively related to depth and Chl *a* concentration (standardized regression coefficient 0.35 and 1.02, respectively) and negatively related to foraminiferan biomass (standardized regression coefficient -0.43). The model explained 57 % (adjusted R^2) of the variance in our data. Foraminiferan biomass and Chl *a* concentration were also retained in the following three subset models with either depth and infaunal biomass, none, or infaunal biomass as additional predictor variable.

The best open-water model, explaining 74% (adjusted R^2) of the total variance, did also encompass three predictive variables (Table 1.3). Again, Chl *a* concentration exhibited the highest relation to benthic carbon remineralisation (standardized regression coefficient 0.63) and foraminiferan biomass was negatively related (–0.23), but this time, infaunal biomass was the third significant variable contributing to the best-subset model (0.25). These three variables were retained in the four best models, with total sediment pigment concentration and/or water depth as additional predictors in the subsequent models, that were disqualified following MC*p* (Table 1.3).

Discussion

Hypothesis 1: Food availability for the benthos increases after the ice melt

Site and season had effects of similar importance on the distribution of total sediment pigment concentration, but their influence on Chl *a* distribution cannot be separated. Water depth seemed to affect both parameters: The lowest concentrations were found at the deepest site in the central Amundsen Gulf and the highest concentration at the shallowest site in Franklin Bay. These results correspond with the general finding that the vertical flux of organic matter decreases with depth (Carmack and Wassmann, 2006; Christensen, 2000).

The significant effect of season on total sediment pigment concentration, i.e., its general increase from ice to open-water season, supports our hypothesis that food supply to benthic communities in the southeastern Beaufort Sea rises after the ice melt characterizing the spring-to-summer transition. The lack of an interaction between site and season indicates that this temporal trend was independent of the significant concentration differences among the sites. A similar conclusion has been reported for vertical flux patterns in the southeastern Beaufort Sea (Juul-Pedersen et al., 2010): sedimentation rates were significantly higher in summer than in fall, but also showed a higher variability

among the different sites in summer than in fall. The importance of seasonal food pulses for the benthos has been recognized since some time (Pfannkuche, 1993), and the pronounced seasonality of the production period and, hence, the vertical flux of organic matter is one of the major factors explaining the tight pelagic-benthic coupling observed in Arctic shelf regions (Grebmeier and Barry, 1991; Klages et al., 2004).

Sediment Chl *a* concentration in the study area, as determined by fluorometry, was slightly higher in 2008 (0.7-3.5 mg Chl *a* m^{-2}) than in 2004 (0-2 mg Chl *a* m^{-2}) (Morata et al., 2008). In Franklin Bay, they were even up to four times higher (7-11 vs 3-4 mg Chl *a* m^{-2}). An upwelling event in late 2007 and early 2008, the year of our study, led to enhanced primary production and vertical export particularly in Franklin Bay and close to the Mackenzie river delta (Tremblay, pers. comm.; Williams and Carmack, 2008), where a higher input of food to the seabed may thus have allowed preserving the seasonal signal. However, the other sites of this study were not affected by this event (vertical flux 38-68 mg POC m^{-2} d^{-1}, Sallon et al., 2011) and were located in an area generally expected to receive less input from the water column than other Arctic regions (Lalande et al., 2009). Moreover, analysis of carbon flux in the central Amundsen Gulf has shown that high pelagic turnover did not allow for intensive organic matter export despite an increased primary production in this area (Sallon et al., 2011; Forest et al., 2011). Despite the interannual difference, the generally low quantity of recently exported 'fresh' material may have prevented a measurable seasonal increase in Chl *a* concentration at the seafloor here.

The detection of a seasonal signal in total sediment pigment concentration but not in Chl *a*, the indicator of fresh material, is not in contradiction. Morata et al. (2010) have demonstrated that a combination of analytical methods were necessary to verify the arrival of a food pulse that had not been detectable using fluorometric analysis of sediment pigments in the course of a spring-to-summer transition. The response of benthic communities to algal input can be rapid but of limited duration (Sun et al., 2007), and we may have sampled some sites after the onset of such a rapid consumption. This would imply a processing of fresh (Chl *a*) to more decomposed (phaeopigments) algal material.

Indeed, we report a tendency of increasing Chl *a* concentration combined with the significant increase in total pigment concentration from spring to summer. Considering a possibly insufficient resolution for the transient signal of sedimentary Chl *a* concentration, our results support the hypothesis of enhanced high-quality food supply to the benthos after the ice break-up that may be rapidly processed by benthic communities.

Our findings also highlight that there is a spatial variability in the importance of the processes driving the food supply to the benthos. The general spatial pattern of sediment pigment concentration reflects differences in primary production and depth at the different sites. Lowest concentrations of sediment pigments were found in the central Amundsen Gulf, where the depth reduces organic matter export (Carmack and Wassmann, 2006). Highest concentrations were found in Franklin Bay and A-CW sites that were situated in or at the margin of the upwelling zone reported for 2008 (Tremblay, pers. comm.), but similar values were reported for most sites at ca. 200 m depth. Whereas Lepore et al. (2007) suggested a lack of spring-to-summer signal for years of enhanced primary production and export in Chukchi Sea, here, the seasonal increase in both Chl *a* and total sediment pigment concentration was highest at sites A-CW and FB (Table 1.2). We would have expected a more evident increase for A-NW in this context, but the late summer sampling date (August) may have allowed for a more complete degradation of algal material since the spring bloom at this site (see above).

Hypothesis 2: Benthic biomass increases after the ice melt

Total benthic biomass did not change significantly after the ice break-up, but did show a tendency to increase. This may reflect a lag between food input and faunal production and reproduction. Metabolic responses and, therefore, carbon remineralisation react more quickly to food inputs than does biomass (Brey et al., 2010). At one site (A-NE), we did observe a seasonal transition from juvenile to adult individuals in polychaete species between the two sampling events, but a quantification of such growth processes is difficult due to the small size of the encountered infauna. The influence of predation has neither been investigated in our study area nor suggested to limit the increase of biomass in

other polar regions (Ambrose and Renaud, 1997, Bluhm and Gradinger, 2008). Moreover, faunal composition also responds to environmental changes on time scales greater than 1 year (Cusson et al., 2007; Piepenburg et al., 2011) and does therefore integrate the effects of past processes that have not been covered during our sampling. It is noteworthy that spatial patterns of biomass did not match those of sediment pigment concentration or carbon remineralisation as can often be expected in polar regions (e.g. Carroll et al., 2008; Witman et al., 2008). Values at FB were not higher than at other sites, and at sites A-NE, A-NW and A-CW biomass increased strongly from spring to summer. Total benthic biomass is only one of several benthic community factors reacting to food supply patterns, as metabolic rates differ widely among species (Michaud et al., 2009). The southeastern Beaufort Sea is one of the most diverse Arctic shelf regions (Piepenburg et al., 2011). Local community composition can be quite variable (Cusson et al., 2007), which involves changes in trophic positions and, therefore, in carbon cycling efficiency (Tamelander et al., 2006; Sun et al., 2009). A better proxy than mere biomass would be achieved if functional composition of benthic communities were considered in the analysis (Bolam et al., 2002; Michaud et al., 2005), and hence, we coarsely separated biomass into infauna and foraminifera for analysis of driving factors.

We did not determine the biomass of microbes and meiofauna, which have higher reproduction and growth rates and are thus more likely to show a detectable short-term biomass increase in response to organic matter input (Rex et al., 2006; Soltwedel, 2000). We did not find an increase in foraminifera biomass over the seasonal transition as it has been reported from other investigations (Altenbach, 1992; Moodley et al., 2002). Our restriction to individuals of macrofaunal size may explain the deviation from processes described for foraminifera communities elsewhere, since total communities in those studies where dominated by meiofaunal species of smaller size and presumably faster metabolic reactions. These differences in community composition likely influence the timing and amplitude of the benthic response to seasonal food input (Renaud et al., 2007a).

Hypothesis 3: Benthic carbon remineralisation increases after the ice melt

In our 2008 data, the spatial and temporal distribution of benthic carbon remineralisation largely reflected that of sediment pigment concentration: there were significant effects of both season and site, with the latter being even more pronounced than the former. There was no interaction between the two effects, indicating that the carbon cycling generally increased from spring to summer, independent from spatial differences in the extent of this rise. Our results, therefore, support the hypothesis that benthic carbon remineralisation in our study area increases after the ice break-up.

Microcosm incubations are a widespread and robust method for benthic community metabolic measures (e.g. Tengberg et al., 2004) and produce reliable estimates for benthic carbon remineralisation (Renaud et al., 2007a). During our measurements, the temperature of the experiments was slightly higher (max. 4 °C) than in situ bottom water temperature as measured 10 m above ground during CTD casts. Even though this might influence the accuracy of our absolute carbon cycling estimates (max. 30% overestimation following Q_{10}), it is common practice in Arctic studies to run shipboard incubations between 0 and 4 °C (e.g. Grant et al., 2002; Renaud et al., 2007a). Moreover, temperatures were generally constant for incubations during this study and, hence, did not affect the comparability of the data gained in the course of our study.

Benthic carbon remineralisation rates were lower in summer 2008 (11.6-44.4 mg C m^{-2} d^{-1}) than those observed by Renaud et al. (2007a) in the same region in summer 2004 (18.0-58.8 mg C m^{-2} d^{-1}). At first glance, this seems to be in contradiction to the primary production reported to be higher in 2008 than 2004 (Forest et al., 2011). However, carbon turnover in the water column has also been reported to be particularly high in 2008 leading to vertical fluxes similar to those in 2004 and a weaker pelagic-benthic coupling (Sallon et al., 2011). Our data suggest that food availability at the seafloor was comparable or even higher than in 2004 (0.7-3.5 in 2008 vs 0-2 mg Chl *a* m^{-2} in 2004). The lower benthic activity observed in 2008 may be explained by two other factors. First, experimental studies have emphasized the fast but also rather short-term response of

sediment community respiration to organic matter input (Graf, 1992; Sun et al., 2007). The signal may already be lost after two weeks. It is possible that most of our summer data were obtained in a later, more declined or beginning phase of benthic activity, and that data from 2004 were rather obtained during the peak response shortly after the sedimentation pulse. This may also explain the important differences of organic matter degradation between sites compared to seasons. Nevertheless, we are confident that our sampling design was appropriate to detect the benthic response to food supply. The general increase in sediment pigment concentration during the open-water period covered by our study indicates that the effects of enhanced food supply during and/or shortly after the ice melt were still measurable. Organic matter export to the seafloor occurs over several days to weeks, and it is likely that the Arctic benthic communities maintain the shift from 'winter to summer mode' for more than 2 weeks, particularly if high-quality food (Chl *a*) is still available. Second, the difference in benthic activity patterns between 2004 and 2008 may also be caused by differences in faunal composition. The results of Michaud et al. (2005) show that sediment oxygen uptake is strongly influenced by the functional groups of species present. Renaud et al. (2007a) have reported very high densities of amphipods at some sites in 2004, which were never observed in 2008. However, more data on faunal composition are needed to test this hypothesis.

The significant differences between sites highlight the amount of spatial variability in parameters influencing the benthic activity such as vertical export, depth and other biotic as well as abiotic factors. Tamelander et al. (2006) have demonstrated important spatial variability in pelagic-benthic coupling on the northwestern Barents Sea, ultimately influencing the benthic food web. The spatial pattern of benthic carbon remineralisation in our study is generally congruent with that in sediment pigment concentration, and highest values were observed in Franklin Bay, the shallowest site (FB), and lowest values at the deepest site in the central Amundsen Gulf (A-CC). Carbon cycling increase from spring to summer was significantly greater at FB than at all other sites, indicating that not only water depth but also other parameters are involved. Primary production and vertical export was higher at FB than in other regions of the southeastern Beaufort Sea (Tremblay, pers.

comm.), and we may have been sampling closer to bloom conditions that at other sites. This may lead to a generally higher benthic activity. The interplay of food quantity, quality and benthic community composition needs to be considered for the explanation of spatial patterns in benthic carbon remineralisation.

Hypothesis 4: Spatial variability of benthic carbon remineralisation is determined by both food availability and benthic biomass

In our data, the importance of the factors driving benthic carbon remineralisation slightly changed in the course of the transition from ice-covered conditions in spring to open-water conditions in summer: In both spring and summer, sediment Chl *a* concentration was the most important predictor. In summer, macrobenthic infauna biomass was a secondary significant predictor and foraminiferan biomass retained in the model; in spring foraminiferan biomass was identified as second significant and depth as additional third factor affecting carbon cycling.

A number of studies have described the significant impact of water depth and benthic food availability on carbon remineralisation (Bessière et al., 2007; Graf 1992; Renaud et al., 2007a, 2008). In a study ranging down to 3650 m depth, besides these two factors, benthic biomass was found to be correlated to benthic carbon remineralisation (Clough et al., 2005). Our results partly corroborate these, but also suggest that depth does not directly predict spatial patterns of benthic carbon cycling on the southeastern Beaufort Sea shelf. The general relationship between water depth and sediment pigment concentration (Ambrose and Renaud, 1995; Renaud et al., 2007a) and between water depth and benthic biomass (Conlan et al., 2008) on Arctic shelves has been reported. It is likely that depth had an indirect influence on benthic carbon remineralisation via other parameters during our study, and its inclusion in the best spring model only indicates the dominating influence of other parameters on spatial variability and the aforementioned effects of local processes (e.g. in Franklin Bay) in summer. Areas of enhanced primary production and pelagic-benthic coupling can create 'hotspots' of benthic processes, irrespective of water depth (Grebmeier et al., 2009; Witman et al., 2008). In the low-production ice-covered season,

when food input to the benthos is generally low and limits benthic activity at all sites, the quantity of high-quality food is the most important driver. After the ice melt, sufficient fresh detritus is reaching even greater depths and the level of benthic activity generally rises (Renaud et al., 2008). The metabolic rate is still primarily determined by the actual availability of high-quality food rather than by total sediment pigment concentration (Sun et al., 2009). The significance of infaunal biomass in summer only could be explained by a dormant stage of organisms during starvation periods. The consistent negative effect of foraminiferan biomass on benthic carbon remineralisation in both spring and summer raises questions on the metabolic mechanisms in this group. Recently, Piña-Ochoa et al. (2011) have described use of denitrification processes by many foraminiferan species. This could imply the respiration of nitrate rather than oxygen from the water phase, but it is still unclear, whether foraminiferan denitrification is restricted to anaerobic conditions (Høgslund et al., 2008; Piña-Ochoa et al., 2011). Depending on the oxygen penetration of sediments, which is generally deeper in greater water depths, foraminifera can be abundant down to more than 5 cm sediment depth (Fontanier et al., 2005). Also, the importance of smaller organisms as compared to macrofauna increases with water depth, most likely caused by the limited supply of food in terms of quantity and quality (Clough et al., 2005; Piepenburg et al., 1995; Rex et al., 2006). As their abundance is higher at deeper sites, benthic carbon remineralisation seems to decrease with foraminiferan biomass. Foraminifera are often neglected in studies on benthic macrofauna, due to the high effort for sorting specimens (Soltwedel, 2000; Wollenburg and Kuhnt, 2000). Clough et al. (1997) conducted one of the few studies recording foraminifera and macrofauna in conjunction with benthic processes in the Arctic. However, foraminiferan contribution to the variability in benthic processes was not statistically analysed, and their contribution to benthic carbon remineralisation was not measured in their study. As demonstrated by Gooday et al. (2009) for the deep sea, the size and abundance of macrofaunal foraminifera in Arctic environments imply the need to consider this parameter in the examination of benthic processes.

Conclusions

We hypothesized that an increase in food availability is the prime cause for the general rise in benthic carbon remineralisation after the ice melt in open-water conditions. This hypothesis is not only supported by the concurrent spring-to-summer increase in sediment pigment concentrations and benthic carbon remineralisation but also by the great importance of Chl *a* in predicting benthic carbon cycling. Our results of the two regression models also support our hypothesis that both food supply to the benthos and benthic biomass are the most important determinants for benthic carbon remineralisation, and their different spatiotemporal patterns during this study imply that they are not directly correlated. Overall, these findings indicate the importance of biotic parameters rather than an abiotic factor such as depth in determining the spatial variability of benthic carbon remineralisation, particularly on a regional scale like in our study. The general relationship between food supply and benthic metabolism in seasonally ice-covered polar shelf seas may be regionally modified by the composition of the benthic community. If we assume that a decrease in ice cover accompanied with enhanced pelagic recycling will lead to rather degraded organic matter exported to the benthos over a longer season, we can expect an increase in competition for quality food among benthic communities. Thus, climate changes may favour a shift in community composition towards boreal species on Arctic shelves.

To better understand the effects of the underlying factors driving the spatial and seasonal variability of benthic processes, analyses of the relationship between spatial patterns and annual-to-decadal changes in seasonal dynamics are necessary. The faunal composition of benthic communities represents a long-term integration of environmental conditions, and the significant role of infauna for spatial variability in our study emphasizes that differences in benthic community composition influence carbon cycling at the seafloor. Our findings strongly suggest that it is important to consider the interplay of seasonal dynamics and spatial patterns, involving fast-changing factors such as food supply and slow-changing variables such as benthic community composition over different years,

when evaluating shifts of benthic ecosystem processes in relation to the rapid decline of sea ice in the Arctic.

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CHAPITRE 2

MULTIVARIATE BENTHIC ECOSYSTEM FUNCTIONING IN THE ARCTIC - BENTHIC FLUXES EXPLAINED BY ENVIRONMENTAL PARAMETERS IN THE SOUTHEASTERN BEAUFORT SEA

RÉSUMÉ DU DEUXIÈME ARTICLE

The effects of climate change on Arctic marine ecosystems and their biogeochemical cycles are difficult to predict given the complex physical, biological and chemical interactions among the ecosystem components. To predict the impact of future changes on benthic biogeochemical fluxes in the Arctic, it is important to understand the influence of short-term (seasonal to annual), long-term (annual to decadal) and other environmental variability on their spatial distribution. In summer 2009, we measured fluxes of dissolved oxygen, nitrate, nitrite, ammonia, soluble reactive phosphate and silicic acid at the sediment-water interface at eight sites in the southeastern Beaufort Sea at water depths from 45 to 580 m to address the following question and hypotheses using a statistical approach: (1) What is the spatial variation of benthic boundary fluxes (sink and source)? (2) The classical proxy of benthic activity, oxygen flux, does not determine overall spatial variation in fluxes. (3) A different combination of environmental conditions that vary either on a long-term (decadal) or short-term (seasonal to annual) scale determine each single flux. And (4) A combination of environmental conditions varying on the short and long-term scale drive the overall spatial variation in benthic boundary fluxes. The spatial pattern of the measured benthic boundary fluxes was heterogeneous. Multivariate analysis of flux data showed that no single or reduced combination of fluxes could explain the majority of spatial variation. We tested the influence of eight environmental parameters: sinking flux of

particulate organic carbon above the bottom, sediment surface Chl *a* (both short-term), porosity, surface manganese and iron concentration, bottom water oxygen concentrations (all long-term), phaeopigments (intermediate-term influence) and $\delta^{13}C_{org}$ (terrestrial influence) on benthic fluxes. Short-term environmental parameters were most important for explaining oxygen, ammonium and nitrate fluxes. Long-term parameters together with $\delta^{13}C_{org}$ signature explained most of the spatial variation in phosphate, nitrate and nitrite fluxes. Sediment pigments and $\delta^{13}C_{org}$ levels in surficial sediments were most important to explain fluxes of silicic acid. The overall spatial distribution of fluxes could be best explained (57 %) by the combination of sediment Chl *a*, phaeopigments, $\delta^{13}C_{org}$, surficial manganese and bottom-water oxygen concentration. We conclude that it is necessary to consider long-term environmental variability in the prediction of the impact of ongoing short-term environmental changes on the flux of oxygen and nutrients in Arctic sediments. Our results contribute to improve ecological models predicting the impact of climate change on marine ecosystems functioning..

Keywords: Benthic ecosystem functioning, nutrient fluxes, Arctic, spatial variation, environmental factors, multivariate analysis

This article was co-authored by myself, Prof. Gwenaelle Chaillou, Dr. Alexandre Forest, Prof. Dieter Piepenburg and Prof. Philippe Archambault. As first author, I conducted the experimental work, most of the laboratory and statistical analyses and wrote the publication. Prof. Gwenaelle Chaillou contributed to the original idea and the writing. Dr. Alexandre Forest provided data on Vertical POC fluxes and participated in the production of the manuscript. Prof. Dieter Piepenburg and Prof. Phillipe Archambault participated in the production of the manuscript. The manuscript has been accepted for publication in *Biogeosciences Discussions* in November 2012. Parts and short versions of this publication have been presented at the following conferences: (1) *Malina Plenary Meeting* in Villefranche-sur-mer (France) in May 2010 and (2) *Goldschmidt 2012 - Earth in Revolution* in Montreal (Canada).

MULTIVARIATE BENTHIC ECOSYSTEM FUNCTIONING IN THE ARCTIC - BENTHIC FLUXES EXPLAINED BY ENVIRONMENTAL PARAMETERS IN THE SOUTHEASTERN BEAUFORT SEA

Introduction

Increased effort is put into estimating climate change effects in Arctic ecosystems (ACIA, 2004; Wassmann et al., 2011; Barber et al., 2012). Contrary to multilevel analyses of pelagic processes (Forest et al., 2011; Tremblay et al., 2011), few studies have tried to link environmental conditions to benthic ecosystem functioning in terms of multiple processes in the Arctic (Schmid et al., 2009). Marine sediments play a pivotal role in the remineralisation of the organic matter settling to the seafloor. They can be both a major source of nutrients and carbon to the overlying water column or / and a significant sink (Schulz, 2006). Typically, a significant fraction of exported organic matter undergoes biologically mediated degradation and oxidation through a complex web of redox reactions, while a small remaining fraction is permanently buried (Berner, 1980). Determining the spatial variation and partition between source fluxes from and sink fluxes to the sediments is important for improving our understanding of regional biogeochemical cycles (Ebenhöh, 1995; Zabel and Hensen, 2006), and only few data is available from the Arctic regions being particularly sensitive to climate change (Chang and Devol, 2009; Darnis et al., 2012; Davenport et al., 2012; Rysgaard et al., 1998).

Oxygen uptake is often used as a proxy of total benthic ecosystem functioning, more precisely of activity and remineralisation (Glud, 2008; Hensen et al., 2006; Holstein and Hensen, 2010; Wenzhöfer and Glud, 2002). But evidence is increasing, that benthic nutrient remineralisation is not directly correlated with oxygen uptake, particularly in coastal and shelf environments (Braeckman et al., 2010; Davenport et al., 2012; Holstein and Hensen, 2010; Michaud et al., 2009; Robert et al., 2012).

A wide range of environmental factors influence benthic processes. Determining their relative importance is difficult due to the number and complexity of biotic and abiotic interactions among the processes involved (Godbold and Solan, 2009). Organic carbon

content in sediments has been proposed to be the principal driver of benthic remineralisation. Several different metabolic pathways contribute to the degradation of organic carbon, with oxygen, nitrate, manganese, iron and sulphate being most important agents of remineralisation (Canfield et al., 1993; Froelich et al., 1979). Their relative importance varies temporally and spatially due to changes in environmental conditions. Thus, organic carbon content of sediments seems less predictive of benthic remineralisation (Rysgaard et al., 1998) than the quantity of fresh organic matter deposited on the seafloor (Chang and Devol, 2009; Link et al., 2011). Also, historical input of organic matter, ambient water oxygen concentration and porosity modifies the oxygen penetration of sediments and therefore its reactivity (Gobeil et al., 2001). Finally, biologically mediated degradation in Arctic marine sediments seems to be enhanced if labile, marine derived matter is present (Sun et al., 2009). Thus, the quality of organic matter at the seafloor will influence the pattern of benthic nutrient remineralisation (Rysgaard et al., 1998).

The continental shelf off the Mackenzie Delta in the Beaufort Sea may be particularly sensitive to climate change: Among Arctic rivers, the Mackenzie is the largest exporter of particulate organic matter and ranks third in total terrigenous organic carbon input (dissolved and particulate) to the Arctic seas (Rachold et al., 2004). Over the last two decades, this region has experienced a significant reduction in summertime ice cover (Galley et al., 2008), an increase in ultraviolet radiation (Bélanger et al., 2006), as well as an earlier onset of primary production in spring (Tremblay et al., 2011). These changes would result in a greater export of terrigenous carbon to the Arctic Ocean (Benner et al., 2004) and shifts in marine produced vertical carbon export (Forest et al., 2011). Direct and indirect effects of these changes on Arctic Ocean biogeochemical cycles are difficult to predict in quantitative terms given the complexity of physical, biological and chemical interactions among ecosystem components. It is clear, however, that the flux of organic matter to coastal and shelf Arctic sediments will be considerably altered, which in turn will severely affect benthic ecosystem functioning, including the processes of nutrient remineralisation. Reducing the current lack of knowledge on benthic boundary fluxes in

Arctic regions, or on their link with environmental changes on different time scales, will help to evaluate biogeochemical budgets on larger time scales.

As part of the larger Malina program (http://malina.obs-vlfr.fr/), which aims to predict Arctic ecosystem reactions to changes in light penetration of the ocean and climate, we want to fill gaps in benthic ecosystem process knowledge. The objective of this study was to determine what drives spatial variation in benthic functioning measured as benthic boundary fluxes in the Beaufort Sea/Mackenzie Shelf. Emphasis is put on the ecological perspective and setting, and a hypothesis-driven approach, using multivariate statistics. Specifically, the following research question (1) and hypotheses (2-4) were addressed: (1) What is the spatial variation of benthic boundary fluxes (sink and source)? (2) The classical proxy of benthic activity, oxygen flux, does not determine overall spatial variation in fluxes. (3) A different combination of environmental conditions that vary either on a long-term (decadal) or short-term (seasonal to annual) scale determine each single flux. And finally (4) A combination of environmental conditions varying on the short and long-term scale drive the overall spatial variation in benthic boundary fluxes.

Material and methods

Study Region

This study was conducted in the southeastern Beaufort Sea with emphasis on the shelf off the Mackenzie Delta (Fig. 2.1). The study area is dominated by coastal shelves and the maximum depth of our study was 580 m on the outer Mackenzie Shelf. Annual primary production ranges from 30 to 70 g C m^{-2} yr^{-1}, indicating generally oligotrophic conditions (Sakshaug, 2004). Rather low primary production daily rates (73 ± 37 mg C m^{-2} d^{-1}) were also found in summer or fall 2005-2007 in the eastern Beaufort Sea (Ardyna et al., 2011). In the Cape Bathurst Polynya at the eastern boundary of the study area, however, rates are apparently higher, reaching 90 to 175 g C m^{-2} yr^{-1} as based on satellite estimates (Arrigo and van Dijken, 2004). Ardyna et al. (2011) reported daily primary production rates of 159 ± 123 mg C m^{-2} d^{-1} in summer and fall, and intensive phytoplankton blooms related

to ice-edge upwelling events were documented for coastal regions of the Mackenzie Shelf and Amundsen Gulf in 2008 (Mundy et al., 2009; Tremblay et al., 2011). An annual vertical POC flux of 1.6–1.8 g C m^{-2} yr^{-1} and 2.4 g C m^{-2} yr^{-1} was estimated at 200 m water depth for the Mackenzie Shelf and the Cape Bathurst Polynya, respectively (O'Brien et al, 2006; Forest et al., 2007; Lalande et al., 2009). Seafloor sediments are dominated by fine-grained material that is usually composed of more than 70 % silt and clay (Conlan et al., 2008). Sediment characteristics indicate that organic carbon at the seafloor is to a large part derived from either the Mackenzie River plume and erosion (O'Brien et al., 2006) or refractory marine material (Morata et al., 2008; Magen et al., 2010; Sallon et al., 2011). The latter dominates the carbon flux in summer and on the eastern shelf (Naidu et al., 2000) whereas on the Mackenzie Shelf carbon of terrestrial origin is abundant in fall (Morata et al., 2008).

Field Sampling

Samples were collected during the Malina program at eight sites ranging in water depth from 47 m to 577 m in July and August 2009 onboard the icebreaker CCGS Amundsen (Table 2.1). At each sampling event ('station'), an USNEL box corer (50 × 50 × 30 cm) was deployed for seafloor sediment collection. From each box core, three sub-cores of ten cm diameter and approximately 20 cm sediment depth were taken for assessing benthic oxygen demand and nutrient remineralisation in microcosm incubations. Six additional sub-cores of 2.4 cm diameter and 8 cm and 1 cm length were taken for determining sediment pigment concentration and water content and sediment solid phase composition, three sub-cores each, respectively (Table 2.1). Samples from the sediment surface (0 to 1 cm sediment depth) of additional sub-cores were stored in pre-weighed plastic vials and frozen immediately at –80 °C for later analysis. Near-bottom water temperature and salinity were determined by the shipboard CTD probe at each station 10 m above the seafloor. Salinity ranged from 32.2 at the shallowest site (47 m) to 34.9 at the deepest site (577 m). Temperature values varied between -1.6 °C and 0.4 °C (Table 2.1).

Sediment Pigment Concentration

Chl *a* and phaeopigment concentrations were analysed fluorometrically following a modified protocol proposed by Riaux-Gobin and Klein (1993) as described in Link et al. (2011): Two grams of wet substrate were extracted with 10 ml 90 % Acetone (v/v) for 24 h at 4 °C, and the supernatant was measured in a Turner Design 20 fluorometer before and after acidification. Chl *a* and total pigment concentration (Chl *a* + phaeopigments) were determined. Quantities are expressed as microgram pigment per gram of dry sediment [$\mu g\ g^{-1}$].

Table 2.1: Station list. Labels, data of sampling, geographic position, bottom-water temperatures and salinities, number of within-station replicate samples used to determine benthic boundary fluxes (BBF) and sediment surface properties (Chl *a*, phaeopigments, porosity, manganese and iron oxide). A = Amundsen Gulf, MD = Mackenzie Delta, MS = Mackenzie Shelf/Slope; C, E, N, W = central, east, north, west

Station	Malina Station Label	Date	Depth [m]	Latitude [°N]	Longitude [°W]	Sal_{bot}	T_{bot} [°C]	BBF (n)	Sed Prop (n)
MD-C	390	31/Jul/09	47	70.178	133.569	32.24	-1.3	3	3
MD-W	690	01/Aug/09	55	69.486	137.942	32.49	-1.6	3	3
MD-E	260	04/Aug/09	60	71.269	130.613	32.32	-1.2	3	3
A-NW	110	06/Aug/09	400	71.696	126.477	34.77	0.3	3	3
A-CW	140	07/Aug/09	154	71.285	127.783	33.4	-1.4	1	1
			154	71.285	127.782			2	2
MS-W	680	10/Aug/09	125	69.611	138.235	32.31	-1.3	3	3
MS-C	345	16/Aug/09	577	71.382	132.652	34.86	0.2	3	3
MS-E	235	22/Aug/09	576	71.764	130.766	34.84	0.4	3	3

Particulate surficial sediment composition

Porosity was determined by comparison of weight of wet and dried sediment. Porosity was calculated using a dry sediment density of 2.65 g cm^{-2} (Berner, 1980). The dried solid fraction was homogenised and the water content used to correct the analyses for the presence of sea salt.

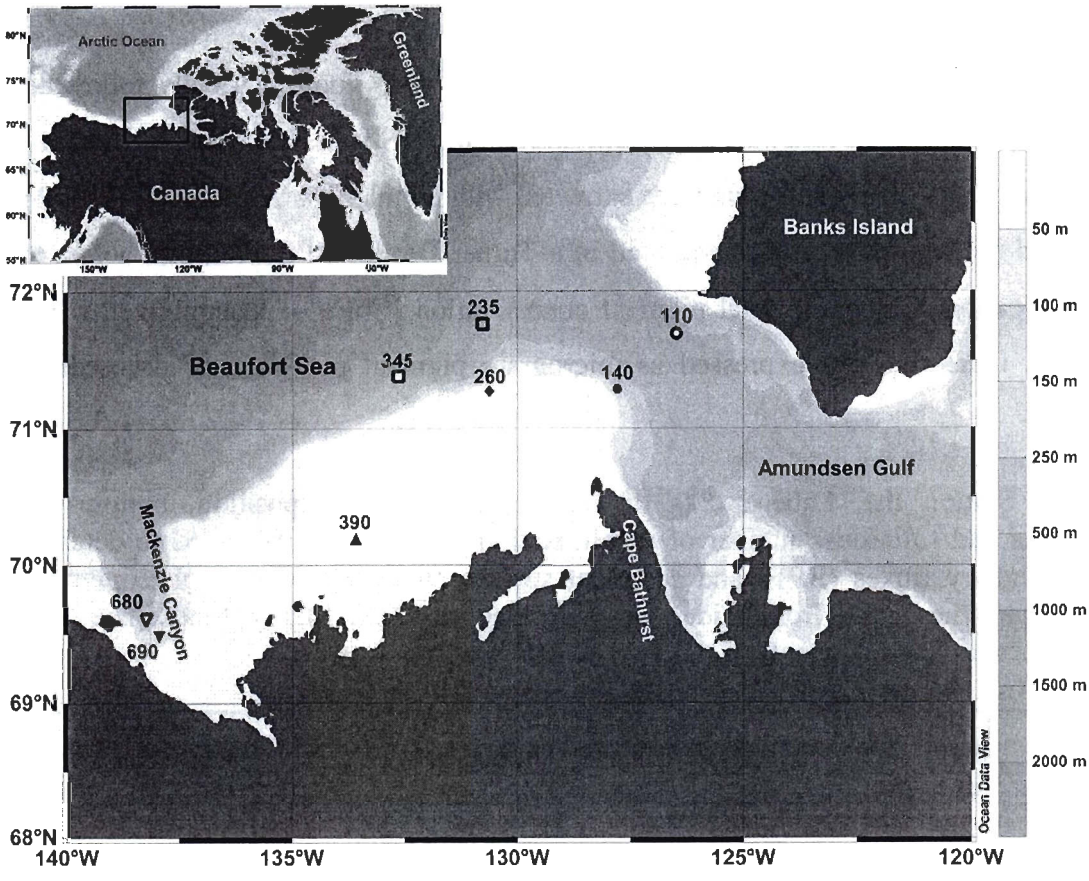


Fig. 2.1: Locations of sites sampled for benthic boundary fluxes during the Malina expedition in the Beaufort Sea in summer 2009

For stable isotope composition analysis, grounded sediments were acidified twice for 48h with a dilute HCl (1N) solution to dissolve solid carbonates. The acid supernatant was decanted and solids rinced with nanopure water and dried. Samples were analysed for $\delta^{13}C_{ORG}$ and $\delta^{15}N$ with a CF-IRMS (continuous-flow Isotope Ratio Mass Spectrometry) coupled to a Costech 4010 elemental analyser. Here, we only report the stable isotope signature of $\delta^{13}C_{ORG}$ of the surficial buried organic matter. Data are reported in standard notation in ‰ with respect to V-PDB for carbon. The analytical precision error was lower than 0.3‰ and three internal standards were measured during the isotopic analyses to continuously check the accuracy of the measurements.

Acid soluble Mn- and Fe-oxides were determined on homogenised dried sediments using 1N HCl solution. About 250 mg of dry sample was leached with a 12 ml solution during 24 hours while shaking continuously at room temperature. The centrifuged and filtered solution was then diluted in 0.2 N HCl and analyzed with a flame atomic absorption spectrometer (5100PC Perkin-Elmer). The analytical precisions were better than ±3% and ±7% for Mn and Fe, respectively. Acid soluble Fe (Fe_{HCl}) represents amorphous iron-oxides, FeS, some iron phyllosilicates and iron carbonates. Specific tests on particulate Mn extraction with 1N HCl (Mn_{HCl}) have shown that Mn_{HCl} represents the whole fraction of Mn-oxides and Mn associated with carbonates (Anschutz et al., 2006).

Sinking fluxes of particulate organic carbon (POC) reaching the benthic boundary layer (approximately 20 m above bottom) were derived from a particle size distribution dataset obtained with an Underwater Vision Profiler 5 (UVP5, Picheral et al., 2010) deployed at every station (Table 2.1). Full methodology on the functioning of the UVP5 and on the estimation of sinking POC fluxes can be found in Forest et al. (2012). Briefly, particles in the range 0.08-4.2 mm (in equivalent spherical diameter) recorded with the UVP5 were transformed into sinking fluxes by applying a regional empirical algorithm linking sediment trap fluxes and the UVP5 dataset. The algorithm was calibrated using an optimization function following Guidi et al. (2008) and provided robust agreement between sediment trap POC fluxes and UVP5 POC fluxes ($r^2 = 0.68$, $n = 21$).

Benthic oxygen flux and nutrient remineralisation

Incubations of sediment microcosms were run in a dark, temperature-controlled room (2 to 4 °C) for 24 to 48 h. Prior to the onset of measurements, sediment cores were carefully topped with bottom water collected by the rosette at the same site, and then allowed to acclimate for six to eight hours while being saturated with oxygen to avoid suboxic conditions during incubations. At the onset of measurements, the microcosms were hermetically closed and bubbles were removed. During the incubation, the water overlying the sediment was constantly stirred without resuspending the sediment surface. Total sediment oxygen flux was determined as the change in oxygen concentrations in the water

phase and was measured periodically (2 to 8 h intervals) with a non-invasive optical probe (Fibox 3 LCD, PreSens, Regensburg, Germany). During incubations, oxygen concentration never decreased by more than 25 % in order to avoid anoxic conditions and biogeochemical transformations. Hall et al. (1989) demonstrated the importance of maintaining the O_2 supply to obtain consistent and relevant data during core incubations.

To determine changes in nutrient concentration, samples of the overlying water phase were taken at three times during the incubation, including the onset and end. Water samples withdrawn for analysis were immediately replaced by an equivalent volume of bottom water of known nutrient composition. The total amount of water withdrawn and replaced during each sampling never exceeded 10% of the total overlying water volume to prevent artefacts. Three additional incubation cores containing bottom water only acted as controls for assessing the oxygen consumption and nutrient changes due to processes within the water column or sample handling. Oxygen and nutrient fluxes were determined as the slope of the linear regression of the oxygen and nutrient concentration on incubation time and corrected for solute concentration in the replacement water. Median flux rates determined in the three control cores were subtracted from each sediment core measure. A positive flux means a release of the nutrient from sediment into the water column.

Samples were filtered through combusted GF/F filters and split into subsamples for nutrient analyses. For NH_4^+ measurements, 6 ml samples were immediately incubated with 3 ml orthophtaldialdehyde solution following an adaptation of the method proposed by Holmes et al. (1999). Samples were analysed using a Turner Design fluorometer 5-6 h after the initiation of colorimetric reaction. Detection limit for ammonium was 0.1 μM. For nitrate, nitrite, phosphate and silicic acid measurements, water samples were frozen at -80 °C and analysed within the following two weeks using an Autoanalyzer 3 (Bran and Luebbe) applying colorimetric methods adapted from Grasshoff et al. (1999). The precision of these methods was ±5%.

Definition of short-term and long-term environmental factors

We used environmental parameters of different temporal variation to explain benthic boundary fluxes. As short-term scale we define seasonal to annual time scales and the parameters sediment surface Chl *a* concentration and vertical POC export. Results reported from different seasons and years in the Beaufort Sea have shown that sediment Chl *a* concentration and vertical POC export vary both over seasons and years (Link et al., 2011; Morata et al., 2008; Renaud et al., 2007a; Forest et al., 2007; Juul-Pedersen et al., 2010; Sallon et al., 2011) respectively. This is likely due to the seasonal and spatial dynamic of primary production and carbon fluxes in the region (Ortega-Retuerta et al., 2012; Tremblay et al., 2011; Forest et al., 2010).

As long-term we define temporal variations of decades and longer. Bottom-water oxygen concentration of shelf waters changes on such time scales (Gilbert et al., 2010), as does iron oxide (Hensen et al., 2006) and manganese oxide concentration (Gobeil et al., 2001; Katsev et al., 2006) in sediments. In open ocean regions, changes in the ocean's dissolved oxygen are likely related to physical processes and thermohaline circulation. The major drivers of these changes are increased temperature, altered hydrological cycles and shifts in wind patterns that alter coastal currents and upwelling formation (Rabalais et al. 2009). The effect of interdecadal changes in deep-water characteristics have recently been proposed to explain a decline in dissolved oxygen saturation in deep waters of both coastal waters (Gilbert et al., 2005; Chan et al., 2008) and open basins (Fukasawa et al., 2004). At the sediment–water interface, the abundance of trace metals such as Mn and Fe-oxides allows to track the depositional redox conditions (Tribovillard et al., 2006). Sedimentary redox conditions reflect the balance between the O_2 diffusing from the bottom water and metabolic aerobic processes that mineralize the labile organic carbon at the sediment-water interface (Canfield et al., 1993; Froelich et al., 1979). Over a period of several decades, the upward migration of sedimentary redox boundary can generate surficial peak of metal-oxides as a result of generally increased water column productivity (Gobeil et al., 2001; Katsev et al., 2006) or progressive decline in the deep water oxygen saturation (Lefort et al., in press). Changes in porosity of sediments depends on the sedimentation rate, which is

generally about 1 mm yr^{-1} in the study area (Richerol et al., 2008) and can therefore also be considered long-term.

Sediment phaeopigment concentration depends on vertical POC flux (short-term) but is also the accumulation of degraded material over several years (Morata et al., 2008). The signature of $\delta^{13}C$ in surface sediments depends on the contribution of terrestrial versus marine produced carbon to the total carbon input and rather indicates input of sediments from the Mackenzie River (Goñi et al., 2005; Magen et al., 2010; Naidu et al., 2000). Therefore, sediment phaeopigment concentration and $\delta^{13}C$ signature are considered 'other' environmental factors..

Statistical analyses

We used best-subset multiple regression analyses to identify potential drivers of each single flux separately. Predicting variables allowed in the model were: Sediment surface Chl *a* concentration, sediment surface phaeopigment concentration, sediment surface porosity, sediment surface manganese-oxides concentration, sediment surface iron-oxides concentration, sediment surface $\delta^{13}C$, bottom water oxygen concentration and vertical flux of POC. Due to independent sampling of environmental and benthic flux data, the median value of each site of each of the predicting variables was attributed to the three flux replicates of each site. This allowed for keeping the high variability of benthic boundary fluxes in the model testing. Analysis of multicollinearity showed that sediment Chl *a* concentration and sinking POC in the lower water column were highly correlated ($R = 0.92$). Nevertheless, both predictors were retained in the initial full multiple regression model to determine which of the two would be predictors in the best solutions. Akaike's Information Criterion (AIC) was applied to choose the best linear model (Akaike 1978; Quinn and Keough, 2002). In none of the best models, both predictors were retained. Normal distribution of the best model's residuals was verified with Shapiro-Wilk's test, and homogeneity of variance was tested using graphical methods (Quinn and Keough, 2002). If distribution of residuals was skewed, natural logarithm transformation was applied to the response variable and/or sediment surface Chl *a* and sinking POC data until assumptions

were met by the best model. Normality could not be achieved for any NO_2^- model, thus only the graphical method was applied. Outliers with severe influence on the model were identified using Cook's Distance (D) and removed if $D > 1$. One outlier in the silicic acid fluxes was found and removed from all further analyses (Table S2.1). We tested for collinearity of variables retained in the best-subset model using the variance inflation factor (VIF), with $VIF > 10$ indicating critical collinearity (Quinn and Keough, 2002). This was not the case for either of the best-subset models.

Principal Component Analysis (PCA) was used to determine the influence (eigenvector) of the six measured benthic boundary fluxes on the ordination of samples in a multidimensional space. Prior to PCA, homogeneity of each variable was assessed using a draftsman plot, and ammonium fluxes were transformed using natural logarithm. Moreover, flux data was standardized using the 'normalise' routine in PRIMER-E (Clarke and Gorley, 2006). No pair of fluxes was correlated with $R > 0.7$, with the exception of nitrate and oxygen ($R = 0.82$).

A stepwise distance-based linear model permutation test (DistLM, McArdle and Anderson, 2001) was performed to identify which set of environmental variables predict the multivariate variation of benthic boundary fluxes, thus taking into account possible interactions between different fluxes (in contrast to the multiple-regression approach described above). The resemblance matrix quantifying the between-samples similarities in terms of all six standardized fluxes was calculated based on Euclidean distances (Clarke and Gorley, 2006). Predicting environmental variables allowed to enter the model were sediment surface Chl *a* concentration, sediment surface phaeopigment concentration, sediment surface porosity, sediment surface manganese-oxide concentration, sediment surface iron-oxide concentration, sediment surface $\delta^{13}C$ and bottom-water oxygen concentration. To represent natural variation as much as possible in the analysis but to avoid arbitrary attribution, each environmental sample of a site was attributed to each replicate flux sample, thus triplicating the original data set. Sinking POC rates were excluded from this analysis due to a lack of replicates and due to its correlation with

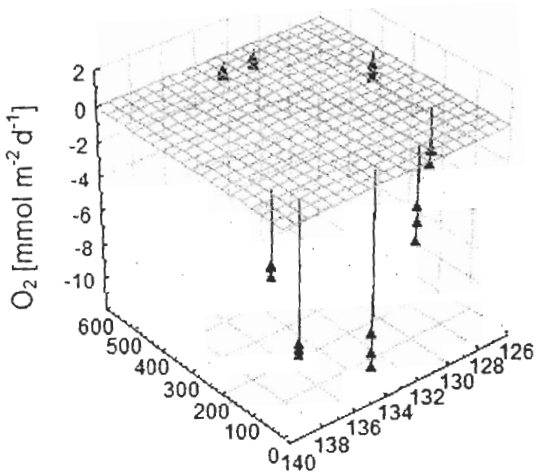
sediment Chl *a*. While the influence of multicollinearity on the model results can be tested for multiple regression (VIF, see above), this is not the case for the DistLM. After assessing normality and collinearity of the other predictor variables using a draftsman plot, sediment Chl *a* data was transformed using the natural logarithm to correct for skewness (Anderson et al., 2008). No pair of variables was correlated by $R > 0.85$ and hence all variables were retained for possible inclusion in the model. The stepwise routine was run employing 9999 permutations and using the AIC_c (Akaike's Information Criterion corrected) selection criterion. The AIC_c was devised to handle situations where the number of samples (N) is small relative to the number (v) of predictor variables ($N/v<40$) (Anderson et al., 2008). Results were visualized with a distance-based redundancy analysis (dbRDA) (Anderson et al., 2008). All multivariate statistical analyses were performed using the PRIMER 6 statistical package with the PERMANOVA+ add-on (PRIMER-E, Plymouth Marine Laboratory, UK).

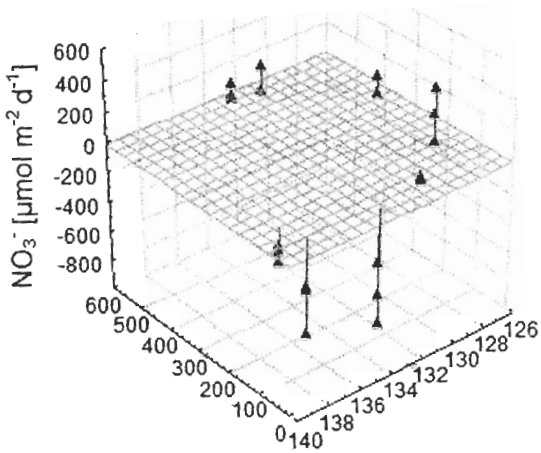
Results

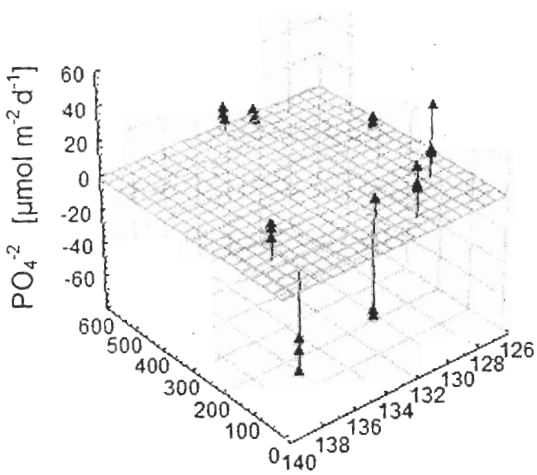
Spatial variability of benthic boundary fluxes

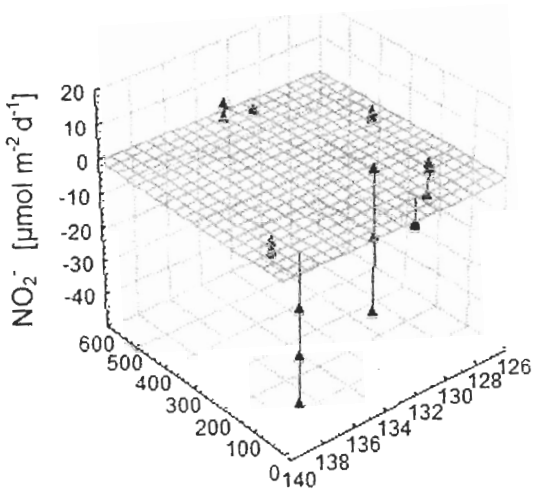
Sediment oxygen uptake varied between 0.5 and 11.5 mmol O_2 m^{-2} d^{-1} with highest values in the shallower central Mackenzie Delta (390) and lowest values on the deeper eastern and central Mackenzie Slope (110, 235, and 345; Fig. 2.2, Table S2.1). This spatial pattern was generally also evident in the release of silicic acid from the sediments (314.5 – 3494.7 µmol m^{-2} d^{-1}, Table S2.1), although fluxes at sites at comparable water depths were higher in the eastern study area (Fig. 2.2).

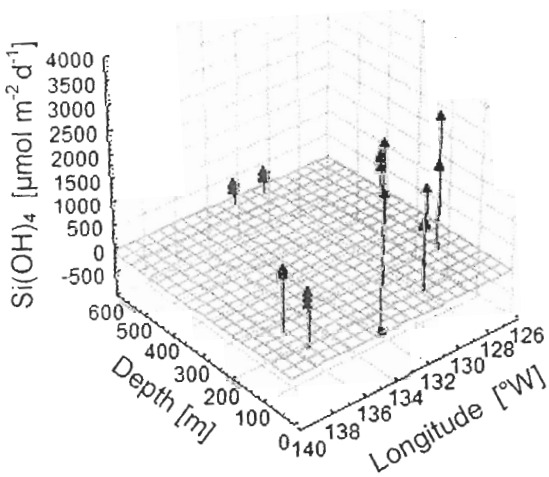
Fig. 2.2: Spatial distribution of benthic boundary fluxes in the southeastern Beaufort Sea (z-axis; O_2 = oxygen, NO_3^- = nitrate, PO_4^{2-} = phosphate, NO_2^- = nitrite, $Si(OH)_4$ = silicic acid, NH_4^+ = ammonium) across a longitudinal (x-axis) and water depth (y-axis) gradient. The values of three replicates from each site are shown in the x-y-z plots. Positive values indicate release from sediments, negative values uptake by sediments, the line is a reference to the zero-plane (values above the plane represent release, below the plane uptake)

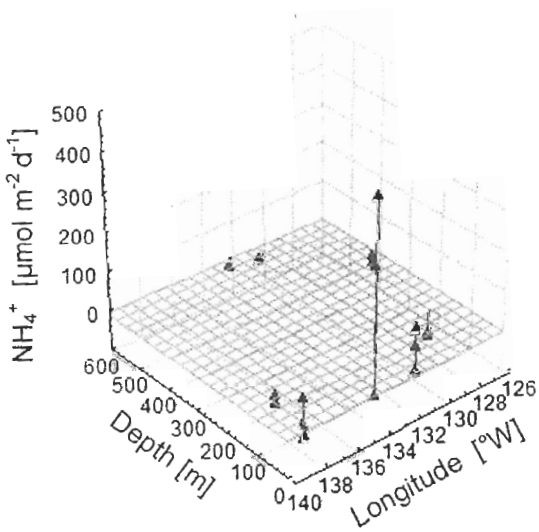

O_2 [mmol m^{-2} d^{-1}]
2
0
-2
-4
-6
-8
-10
600
500
400
300
200
100
0
140
138
136
134
132
130
128
126


NO_3^- [µmol m^{-2} d^{-1}]
600
400
200
0
-200
-400
-600
-800
600
500
400
300
200
100
0
140
138
136
134
132
130
128
126


PO_4^{-2} [µmol m^{-2} d^{-1}]
60
40
20
0
-20
-40
-60
600
500
400
300
200
100
0
140
138
136
134
132
130
128
126


NO_2^- [µmol m^{-2} d^{-1}]
20
10
0
-10
-20
-30
-40
600
500
400
300
200
100
0
140
138
136
134
132
130
128
126


$Si(OH)_4$ [µmol m^{-2} d^{-1}]
4000
3500
3000
2500
2000
1500
1000
500
0
-500
600
500
400
300
200
100
Depth [m]
0
140
138
136
134
132
130
128
126
Longitude [°W]


NH_4^+ [µmol m^{-2} d^{-1}]
500
400
300
200
100
0
600
500
400
300
200
100
Depth [m]
0
140
138
136
134
132
130
128
126
Longitude [°W]

Phosphate was taken up by the sediments at the shallowest sites off the western and central Mackenzie Delta (690 and 390) and mostly released at all other sites (Fig. 2.2). Nitrate was mostly released from the sediments at eastern sites, while the shelf sites off the central and western Mackenzie Delta were characterized by high sediment uptake rates of nitrate (Fig. 2.2, Table S2.1). Uptake fluxes were found in most nitrite measurements, being highest off the shallow Mackenzie Shelf. Ammonium showed highest release rates recorded from station 390 on the shallower central Mackenzie Shelf and highest uptake rates found in the Cape Bathurst Polynya at station 140 (Fig. 2.2, Table S2.1). Within site, variability of phosphate and all three nitrogen-derived fluxes was higher than for silicic acid and oxygen fluxes (Fig. 2.2, Table S2.1).

Fluxes dominating the variation among sites

In the PCA plot, variation was high between the central (390) and western (690) Mackenzie Delta and all other samples, and low among deeper Mackenzie Shelf and Amundsen Gulf samples (235, 345, 110, 140) (Fig. 2.3). The first PCA axis (PC1) explained 46.2% of the total variance in the flux data, and the first three PCA axes (PC1, PC2, and PC3) together explained 88.3 % (Table 2.2). Analysis of the eigenvectors showed that no single flux dominated the multivariate similarity pattern among samples (Fig. 2.3). Oxygen, phosphate and nitrate fluxes were most correlated with the first PCA axis, while silicic acid and ammonium fluxes showed a closer relationship to PC2 and PC3. Nitrite fluxes correlated almost equally with all PCA axes (Table 2.2, Fig. 2.3).

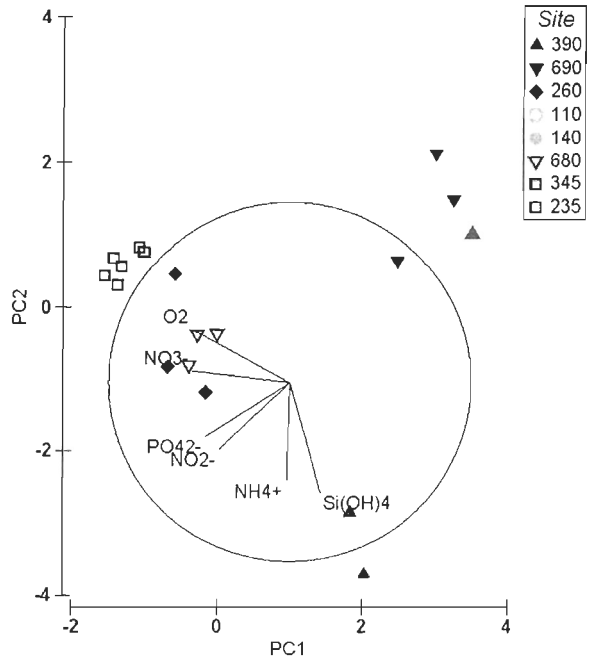


Fig. 2.3: Principal Component Analysis (PCA) plot showing the non-metric multivariate similarity among replicate samples in terms of benthic boundary fluxes. Vectors indicate the direction and strength of each flux's contribution to the overall distribution (Table 2.2). Triangles: shallow Mackenzie Shelf and Delta; circles: Cape Bathurst and Amundsen Gulf region (East); squares: deeper Mackenzie Slope

Table 2.2 Correlation-based Principal Component Analysis (PCA) of normalised benthic boundary fluxes determined in the southeastern Beaufort Sea in July/August 2009. Eigenvalues and % of variation explained by the first 5 ordination axes (PC1, PC2, PC3, PC4, and PC5) is given. Linear coefficients (eigenvector) of each PC are given for each flux

	PC1	PC2	PC3	PC4	PC5
Eigenvalue	2.77	1.64	0.88	0.46	0.22
% variation	46.2	27.4	14.7	7.7	3.6
Eigenvector					
O_2	-0.548	0.295	0.092	0.011	0.055
$Si(OH)_4$	0.170	-0.612	-0.564	0.047	-0.287
PO_4^{2-}	-0.470	-0.306	-0.343	-0.269	0.670
NO_3^-	-0.543	0.065	-0.177	-0.314	-0.677
NO_2^-	-0.394	-0.376	0.252	0.779	-0.062
NH_4^+ (ln)	-0.017	-0.546	0.679	-0.470	-0.062

Environmental drivers of spatial flux variation

Results of environmental parameters used for statistical analyses are presented in Table S2.2. The best models explaining variation in each benthic boundary flux are shown in Table 2.3. Except for ammonium and nitrite fluxes, more than 68 % of the variation in each flux could be explained by the environmental predictors (Table 2.3). Oxygen uptake strongly increased with vertical water-column POC flux, increased with sediment phaeopigment concentration and decreased with the porosity and concentration of iron oxide in surface sediments (adj. $R^2 = 0.98$, $p < 0.001$). Release of silicic acid decreased with phaeopigment concentrations but rose with sediment Chl *a* and bottom-water oxygen concentrations (adj. $R^2 = 0.92$, $p < 0.001$). Phosphate fluxes strongly increased with $\delta^{13}C$ signature and declined with sediment manganese oxide concentrations and with vertical POC flux (Adj. $R^2 = 0.68$, $p < 0.001$). Nitrate fluxes were best predicted by $\delta^{13}C$ signature (positive), sediment manganese oxide and Chl *a* concentration (both negative, adj. $R^2 = 0.81$, $p < 0.001$). Nitrite fluxes increased with $\delta^{13}C$ signature, bottom-water oxygen levels and sediment porosities (adj. $R^2 = 0.50$, $p = 0.002$). Finally, ammonium release was found to strongly increase with Chl *a* and phaeopigment concentrations but to decrease with $\delta^{13}C$ signature (adj. $R^2 = 0.24$, $p = 0.037$).

Table 2.3: Multiple regression analysis of benthic boundary fluxes against environmental factors in the southeastern Beaufort Sea in July/August 2009. Adjusted (Adj.) R^2 and standardized regression coefficients of benthic parameters (Short-term variability proxies: Chl *a* – sediment chlorophyll *a* concentration, POC - sinking POC; medium-term variability proxies: Phaeo – sediment phaeopigment concentration, δ13C – isotopic carbon signature; long-term variability proxies: Mn – sediment surface manganese concentration, Fe – sediment surface amorphous iron concentration, Po - porosity, $O_{2\ bot}$ – bottom water oxygen concentration) predicting each benthic boundary flux. Whole model results are presented for the best-subset solution following Akaike's criterion (Effects – number of parameters included in the model). Absence of standardized regression coefficients indicates that the parameter was not retained in the model. Gray color indicates that the factor was not significant in the model

				Short term		Medium term			Long-term				
Flux	Adj. R^2	F	p	Chl *a*	POC	Phaeo	δ13C	Mn	Fe	P_o	$O_{2\ bot}$	AIC	Effects
$O_{2\ Uptake}$	0.98	237.47	<0.001	*	-1.13 (ln)	0.21			-0.15	-0.26		50.84	4
$\ln(Si(OH)_4)$	0.92	89.61	<0.001	0.34 (ln)	*	0.68					-0.15	-16.21	3
PO_4^{2-}	0.68	17.5	<0.001	*	-0.62 (ln)		1.12	-1.43				206.14	3
NO_3^-	0.81	32.83	<0.001	-0.77	*		1	-1.01				307.38	3
NO_2^-	0.5	6.69	0.002	0.43	*		1.51			0.93	1.46	181.35	4
$\ln(NH_4^+)$	0.24	3.42	0.037	1.41 (ln)	*	-0.89	0.68					72.73	3

Influence of environmental parameters on the overall distribution of benthic boundary fluxes

The best distance-based linear model (DistLM), explaining 57 % of the overall variation in benthic boundary fluxes, is composed of sediment surface Chl *a*, phaeopigment and manganese oxide concentration, $\delta^{13}C$ signature and bottom-water oxygen concentration (Fig. 2.4, Table 2.4). The most important parameters contributing to the first axis of the dbRDA plot (explaining 70.5 % of fitted flux variation), which separates shallower and western sites from deeper and eastern sites, are sediment surface Chl *a* and manganese oxide concentration and bottom-water oxygen concentration (Fig. 2.4). They explain more than 40 % of the total variation (Table 2.4). Sediment phaeopigment concentration and $\delta^{13}C$ signature were most strongly correlated with the second dbRDA axis (explaining 20.8 % of fitted flux variation).

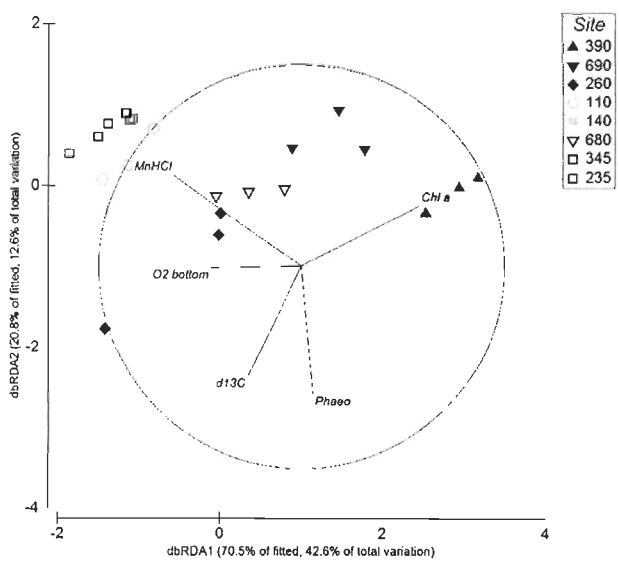


Fig. 2.4: Distance-based Redundancy Analysis (dbRDA) plot of the distLM model based on the environmental parameters fitted to the variation in biogeochemical fluxes (Table 2.4). Vectors indicate direction of the parameter effect in the ordination plot. Chl a = natural logarithm of sediment Chl a concentration; dC13 = $\delta^{13}C$ signature; Phaeo = sediment phaeopigment concentration; MnHCl = sediment surface manganese concentration; O2 bottom = bottom-water oxygen concentration. Triangles: shallow Mackenzie Shelf and Delta; circles: Cape Bathurst and Amundsen Gulf region (East); squares: deeper Mackenzie Slope

Table 2.4: Distance-based linear model (DistLM) of benthic boundary fluxes against environmental drivers determined in the southeastern Beaufort Sea in July/August 2009. Proportion of variance in benthic boundary fluxes explained by environmental variables in stepwise sequential tests following AICc selection criterion. Prop. is the proportion of variance explained by each single variable, Cumul. is the cumulative proportion of variance explained by multiple variables

Sequential tests for stepwise model (Adj. $R^2 = 0.57$)							
Variable	AICc	SS(trace)	Pseudo-F	P	Prop.	Cumul.	res.df
Chl *a*	88.69	122.14	36.72	<0.01	0.344	0.344	70
Phaeo	78.39	37.04	13.05	<0.01	0.104	0.448	69
$O_{2\ bot}$	74.18	16.79	6.38	<0.01	0.048	0.496	68
dC13	66.44	23.33	10.04	<0.01	0.065	0.561	67
MnHCl	61.47	15.11	7.09	<0.01	0.043	0.604	66

Percentage of multivariate flux variation explained by individual axes

	% explained variation out of fitted model		% explained variation out of total variation	
Axis	Individual	Cumulative	Individual	Cumulative
1	70.51	70.51	42.59	42.59
2	20.84	91.35	12.59	55.18
3	7.47	98.83	4.51	59.69
4	1.16	99.99	0.7	60.39
5	0.01	100	0.01	60.4

Discussion

Benthic activity is most often derived from sediment oxygen demand (Graf, 1992; Wenzhöfer and Glud, 2002; Link et al., 2011) and assumed to decrease with increasing depth and distance from the continental source of particles and carbon. But the heterogeneous pattern of oxygen and nutrient fluxes at the sediment-water interface in the Beaufort Sea emphasizes that benthic remineralisation function is more complex than oxygen fluxes. Here we present for the first time a multiple dataset of benthic boundary fluxes, i.e. for oxygen, silicic acid, phosphate, nitrate, nitrite and ammonium, and their relation with environmental variables in the Canadian Arctic. We discuss their spatial pattern and influences of the environment at different time-scales with the aim to estimate

dynamics of benthic ecosystem functioning related to variation in the quality and quantity of organic matter export.

What is the spatial variation of benthic boundary fluxes in the southeastern Beaufort Sea?

In 2009 the spatial pattern of oxygen fluxes was similar to those reported earlier from the region (2003-2004, 2008) (Darnis et al., 2012; Link et al., 2011; Renaud et al., 2007b). All those studies reported highest uptake off the Mackenzie Delta and the Cape Bathurst Polynya. Oxygen demand at shallowest sites (690 and 390) was twice the amount reported from 2004 (Renaud et al., 2007b) and half compared to the upwelling year 2008 (Tremblay et al., 2011). Values from other sites were similar for the three studied years. This indicates that (i) the influence of the Mackenzie Delta increases interannual variability of benthic oxygen uptake at its plume and (ii) that marine influence (such as primary production as in the Cape Bathurst Polynya) is more likely to contribute to the relative spatial distribution of benthic oxygen uptake.

The relatively higher release of silicic acid compared with oxygen uptake in the eastern part of the Beaufort Sea (140) can be explained by the different composition of organic matter exported to the seafloor. First, terrestrial input of organic material is high close to the Mackenzie Delta and along the Tuktoyaktuk Peninsula due to the strong influence of the Mackenzie River plume (Macdonald et al., 2004; Magen et al., 2010). This may increase the input of inorganic silicates (Juul-Pedersen et al., 2008), but these are unlikely to be biologically remineralised at the seafloor. Second, primary production in the Cape Bathurst Polynya area has a higher diatom contribution (Ardyna et al., 2011), which allows for an increased fresh silicic shell export (Simpson et al., 2008). Indeed, Sampei et al. (2011) identified the Cape Bathurst vicinity as a unique zone in biogenic silicate export out of the euphotic zone, with rates roughly one order of magnitude higher than elsewhere across the southeast Beaufort Sea.

Nitrate was replenished at the benthic boundary in deep waters of the slope and in the Cape Bathurst Polynya area (sites 235, 345, 110, 140), while sediments on the shallow Mackenzie Shelf (sites 390, 690, 680) act as sink. On the shallow Mackenzie Shelf, low

oxygen penetration depth (> 1 cm) and a steep gradient in nitrate concentration have been reported, indicating a redox horizon close to the sediment surface (Magen, 2009). Nitrate and nitrite uptake with denitrification processes at the top of the sedimentary column are typically encountered in sediments receiving excess organic matter such as shallow Arctic shelves and continental shelves affected by large river outflow (Hyacinthe et al., 2001; Chang and Devol, 2009; Hulth et al., 2005). Such an input of excess organic matter has also been found during the Malina study (Forest et al., 2012). Nitrate release in the other areas was also consistent with oxygen-saturated degradation. The highest nitrate release in the Cape Bathurst Polynya area (site 140) supports the findings of Simpson et al. (2008), who explained excess nutrient concentrations in the deep Amundsen Gulf water with degradation of more available fresh matter.

The generally low nitrite flux reflects its role as an intermediate product of nitrogen compound transformations. Highest uptake rates were linked to sites with high nitrate uptake or low nitrate release.

The pattern of ammonium effluxes, which are mainly originated from the anaerobic mineralization of organic N, is probably explained by the presence/absence of efficient oxidative barriers at the top of the sedimentary column, such as oxygen and Mn-oxides (Luther et al., 1997; Anschutz et al., 2000; 2005). Highest ammonium effluxes were linked to sites where high organic matter input favours the shallowest oxygen penetration depth and thin Mn-oxides rich horizon, e.g., site 390 (Magen, 2009). The upward migration of ammonia to the bottom water probably promoted denitrification processes at the sediment interface at these sites. The within-site heterogeneous patterns of ammonium fluxes could be due to physiological responses of different macrofaunal species or densities in the cores (Braeckman et al., 2010), which are not available for our study.

Phosphate uptake from the two shallowest sites near the Mackenzie River delta may again be linked to the low oxygenation, a history of high organic matter input, and to the accumulation at the interface of newly formed reactive iron-oxides with high capacity to sorb phosphate (Hensen et al., 2006; Magen, 2009). Sediment phosphate release can be

explained by either a lost of the sediment capacity to adsorb remobilised phosphate or a production of phosphate via aerobic organic matter mineralisation, or both. Desorption from particulate Fe-oxide when sediment Fe-oxide and associated phosphate are exposed to overlying water with lower dissolved P concentrations relative to pore water (Ruttenberg and Sulack, 2011) can also contribute to phosphate release at the sediment-water interface. The highest phosphate effluxes in the Cape Bathurst Polynya (sote 140) probably reflected an increased oxic degradation of fresh matter, as Davenport et al. (2012) observed on the productive Bering Shelf.

Benthic boundary fluxes of silicic acid, oxygen and phosphate in 2009 were in the range of those reported for the region in 2008 (Darnis et al., 2012). It is noteworthy that phosphate was released from shallow Mackenzie Shelf sediments during the upwelling year 2008 and that notably less silicic acid was remineralised in the Cape Bathurst Polynya area in 2008. The increased remineralisation of silicic acid could be explained by the accumulation of excess biogenic silica following vertical export in the highly productive upwelling year of 2008. Phosphate on the other hand is more immediately remineralised from organic matter and the release in 2008 could represent a more short-term reaction to organic matter input from the upwelling year. Concentrations of nutrients at the onset of experiments were in the range described for deeper waters in the study region (Simpson et al., 2008). We therefore consider the described spatial pattern of fluxes a realistic estimate. Seasonal changes in nutrient fluxes have been shown in macrofauna nearshore experiments (Braeckman et al., 2010) and can be found in the Bering and Chukchi Sea (Chang and Devol, 2009; Davenport et al., 2012). Here we report nutrient fluxes and mechanisms for the late summer. Considering the seasonal effect in benthic polar systems (Lepore et al., 2007; Link et al., 2011), lower input of fresh organic matter in winter might therefore be accompanied by a different oxygen, ammonium and silicic acid fluxes.

When considering all fluxes synchronously, site 390 can be well separated from 690, these two are different from the lower Mackenzie Shelf (site 260 and 680), which finally can be separated from the Cape Bathurst Polynya site (110 and 140) and the deeper

Beaufort slope sites (235 and 345) in their remineralisation functioning (see also Fig. 2.3). This spatial pattern has also been found using lipid biomarker analyses conducted on sediment samples collected at some of the sites we studied (Rontani et al., 2012, Tolosa et al., 2012). Particularly high concentrations of autochthonous fresh material derived from diatom production were found at site 390, with decreasing concentrations farther north from the Mackenzie Delta (Rontani et al., 2012; Tolosa et al., 2012).

We conclude that high oxygen demand, nitrate and phosphate uptake prevail in proximity to the Mackenzie outflow, with high ammonium and silicic acid release at the central Mackenzie Delta (site 390), while benthic activity replenishes bottom water with silicic acid, nitrate and phosphate in deeper waters and particularly in the productive Cape Bathurst Polynya area.

The classical proxy of benthic activity, oxygen flux, does not determine overall spatial variation in fluxes

Although sediment oxygen consumption is widely used to described benthic remineralisation function (Grebmeier et al., 2006b; Glud, 2008; Michaud et al., 2005; Holstein and Hensen, 2010), our results confirm this hypothesis and show that differences in benthic remineralisation including six major fluxes are not dominated by oxygen flux. In our study, the major differences between the shallow Mackenzie Shelf and all other sites are equally based on different oxygen, nitrate and phosphate fluxes while the eastern Mackenzie Shelf remineralisation differs greatly from the central shelf in silicic acid and ammonium release. Sampling sites in the Cape Bathurst Polynya and on the western Mackenzie slope were also distinct from all deeper sites with respect to silicic acid and ammonium release. Clearly, oxygen uptake alone cannot describe the spatial pattern of benthic ecosystem functioning in our region. While oxygen uptake is often related to organic matter degradation (e.g. Glud, 2008), further factors influence the quantity and quality of other nutrient remineralisation.

Recent experimental studies have shown that benthic fluxes other than oxygen, e.g. silicic acid or ammonium, respond to treatment of different organic matter input (Callier et

al., 2008; Richard et al., 2007). Such effects have been related to particular species present in treatments, which influence microbial activity (Michaud et al., 2009; Robert et al., 2012). Although we can assume different benthic faunal composition on the Mackenzie Shelf, slope and Cape Bathurst area (Conlan et al., 2008), we do not know how each Beaufort Sea species influences each flux, and even less how they interact with the benthic microbial community. Hence, our results suggest that multiple fluxes need to be considered when the spatial variability of benthic ecosystem functioning in terms of nutrient replenishment is evaluated – whatever factors influence the spatial pattern of benthic nutrient remineralisation.

A different combination of environmental conditions that vary either on a long-term (decadal) or short-term (seasonal to annual) scale determine each single flux

The heterogeneous spatial pattern of benthic boundary fluxes announces the complexity of different factor combinations determining each single flux. Our results of multiple regression analysis support our hypothesis. They show that different subsets of environmental factors can explain spatial variation of different single fluxes, to a surprisingly high part (up to 98%).

While short-term environmental conditions do always explain part of the variation, a large sinking particle flux and an associated increased concentration of sediment Chl *a* most strongly increase oxygen uptake and ammonium release. Observational as well as experimental studies have already demonstrated rapid response of benthic communities to food input (Pfannkuche, 1993; Sun et al., 2007). Ammonium release has been linked to oxic degradation of high quality organic matter by bacterial or faunal communities in shallow and Arctic sediments (Rysgaard et al., 2004). The low explicative power of the best model for ammonium fluxes (24%) indicates that other factors not identified here were playing a substantial role in driving its spatial variability. The faunal composition, which has important effects on ammonium release by sediment oxygenation and bioturbation, might be one of these lacking measurements (Braeckman et al., 2010; Laverock et al. 2011; Piot, 2012).

Environmental parameters of long-term variability (e.g. Mn_{HCl}, porosity, bottom water oxygen) are powerful predictors of phosphate, nitrate and nitrite fluxes, when the origin of organic matter (terrigenous vs marine) is simultaneously considered. This combination may reflect the long-term influence of terrigenous matter sedimentation from the Mackenzie River (Macdonald et al., 2004). The long-term input of organic matter, porosity and surrounding bottom water oxygen concentration limit the depth of the sediment oxic layer. Also, the manganese oxide rich horizon with higher surficial Mn_{HCl} indicates a degradation of organic matter under suboxic conditions during the last decades, which is capable to produce upward dissolved Mn flux that precipitates at the sediment interface (Aller, 1988). These redox conditions also control denitrification and phosphate binding processes and seem to be more important for NOx and phosphate release than the input of fresh marine matter.

We would have assumed that silicic acid release was positively related to Chl *a* and phaeopigment concentration, since we considered sediment pigments a proxy of detrital input. Following dissolution kinetics, silicic acid release supposedly increases with silicate input (Tréguer et al., 1995), and we assumed that more detrital material sinking to the seafloor implies a high silicate input to sediments. However, phaeopigments at the seafloor reflect both silicic and non-silicic detrital material. Possibly, the input of terrigeneous phaeopigment-loaded material from the Mackenzie is higher towards the western part of the Mackenzie plume (Sampei et al., 2011). Phaeopigment-enriched sediments could then represent diatom-poor organic matter input, and would therefore not lead to increased silicic acid release. Recently, Holstein and Hensen (2010) have also demonstrated the importance of bacterial silicate release in oxygenated sediments. Bacterial biomarker concentrations were more abundant in sediments with higher fresh labile matter (Chl *a*) compared to the total input of organic matter (Tolosa et al., 2012). These observations would further explain why an increase in silicic acid release was found in association with increasing Chl *a* and decreasing phaeopigments in our study.

In summary, while short-term factors such as fresh marine matter enhance the oxic degradation and nutrient replenishment, long-term factors reflecting decadal-scale input of organic matter dominates the remineralisation of NO_x and phosphate on the southeastern Beaufort Shelf.

A combination of environmental conditions varying on the short and long-term scale drive the overall spatial variation in benthic boundary fluxes

Despite the differences in environmental factors explaining each single flux (see above), the majority (57 %) of spatial variation in multiple benthic remineralisation function can be explained by a subset of the following five environmental factors: sediment surface Chl *a* (also a proxy for sinking particle fluxes), phaeopigment and manganese oxide concentration, $\delta^{13}C$ signature and bottom-water oxygen concentration. The similarity of the dbRDA plot and the PCA plot show, that the environmental variables explain benthic flux variation fairly well, with a little less congruence for the shallow Mackenzie sites (Anderson et al., 2008). The input of fresh organic matter (Chl *a*) alone can explain a third of the spatial variation, separating the deeper sites from the shelf and shallow sites, particularly site 390. This stresses the importance of short-term parameters for the estimation of nutrient release from Arctic sediments. The quality of organic matter has repeatedly been related to benthic oxygen demand (Renaud et al., 2007a; Link et al., 2011), infaunal diversity (Conlan et al., 2008) and bacterial activity (Rontani et al., 2012) in the southeastern Beaufort Sea. Assuming the importance of biological activity for phosphate (Davenport et al., 2012), nitrogen derivates (Chang and Devol, 2009; Braeckman et al., 2010) and silicic acid (Holstein and Hensen 2010) release, high Chl *a* concentrations at the seafloor not only provides the fresh matter for bacterial degradation, but it also stimulates benthic ecosystem functioning in terms of biological activity of macrofauna, which additionally enhances nutrient release.

The greater marine fraction and phaeopigment content in organic matter input are the primary determinants of the different benthic boundary fluxes in the Cape Bathurst Polynya area when compared with fluxes close to the Mackenzie Delta. It is clear that locations

influenced by the Mackenzie River plume, which feeds a high sedimentation flux of terrigenous particulate matter (Juul-Pedersen et al., 2010; Magen et al., 2010), will show a distinct benthic ecosystem functioning. Finally, the influence of bottom water oxygenation and manganese oxides along the shelf-basin transect north of station 390 demonstrates how long-term environmental factors drive spatial variation in benthic boundary fluxes. Both these factors relate to mostly geochemical processes in the sediments (Gobeil et al., 2001), and may therefore describe a basic variation, on top of which short-term environmental factors further differentiate benthic fluxes.

About 40 % of the total variation in benthic remineralisation function could not be explained by any of the environmental conditions included in the analysis. The most likely missing factor is faunal or bacterial abundance and composition in the analysed sediment cores. An increasing number of studies report the key role of benthic species for benthic boundary fluxes, particularly through their bioturbation or bioirrigation (Davenport et al., 2012; Kristensen et al., 2012). Benthic fauna thus can locally directly enhance nutrient remineralisation or indirectly by modifying bacterial abundance (Michaud et al., 2009; Piot, 2012). It is noteworthy, that sediment porosity, a major parameter used to calculate diffusive fluxes across the sediment water interface (e.g. Hensen et al., 2006), does not play a significant role in our analysis. Again, this emphasizes the role of biological processes for spatial variation in benthic ecosystem functioning in the southeastern Beaufort Sea.

Conclusions

Can we use environmental factors to predict benthic ecosystem functioning on polar shelves? Although we could explain benthic boundary fluxes to a large part without chemistry-based models, we still cannot answer this question with an unambiguous 'Yes'. But compared to the almost non-existent data of benthic fluxes in the Canadian Arctic, our results provide insights on the spatial gradients and driving factors of biogeochemical fluxes across the benthic boundary on Arctic shelves. In addition, the statistical relations found in the present study might help building more comprehensive ecosystem models that

aim at predicting ecosystem functioning in Arctic shelf waters. We report that in summer, the sediments of the southeastern Beaufort Sea are usually a source of silicic acid, while the Mackenzie Delta is a region of nitrate and phosphate uptake and more marine influenced areas are areas of nitrate release. The dominating role of environmental factors varying on a short-term scale indicates that benthic remineralisation rates in terms of quantity will quite rapidly respond to climate changes. On a longer time scale, if terrigenous matter sedimentation from the Mackenzie River and water temperatures increase with climate change, we can expect a decrease in oxygen concentration of coastal bottom waters and sediments, with the latter shifting from nutrient sources to sinks. The analysis of our results emphasizes the importance of biologically mediated degradation interacting with geochemical processes. Including more specific marker of fresh biologically degradable matter and faunal composition data in benthic boundary flux models should further enhance the predictive power of biological ecosystem models.

ACKNOWLEDGMENTS

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Table S2.1: Fluxes of oxygen (O_2), silicic acid ($Si(OH)_4$), phosphate (PO_4^{2-}), nitrate (NO_3^-), nitrite (NO_2^-), and ammonium (NH_4^+) across the sediment-water interface determined for three replicates at eight stations in the southeastern Beaufort Sea in July/August 2009. * denotes an outlier that has been excluded from statistical analyses following Cook's D analysis

Malina Label	O_2 flux [mmol m^{-2} d^{-1}]	$Si(OH)_4$ [μmol m^{-2} d^{-1}]	PO_4^{2-} [μmol m^{-2} d^{-1}]	NO_3^- [μmol m^{-2} d^{-1}]	NO_2^- [μmol m^{-2} d^{-1}]	NH_4^+ [μmol m^{-2} d^{-1}]
390	-9.51	-352.13	-41.07	-785.06	-25.84	-44.61
	-11.47	3494.65	23.25	-597.91	-4.28	281.00
	-10.59	2478.59	-44.26	-378.09	14.39	443.30
690	-8.84	1171.44	-46.35	-345.32	-43.57	-30.80
	-8.13	1082.16	-57.66	-631.51	-15.90	-66.95
	-8.48	947.69	-39.14	-324.24	-29.15	31.38
260	-5.41	2092.55	17.29	10.59	-7.10	21.24
	-4.29	1347.74	27.55	21.24	-7.49	60.89
	-3.42	1377.07	15.51	41.35	-7.94	-53.54
110	-0.98	867.21	3.21	90.24	-3.24	4.35
	-1.31	763.65	0.38	-27.85	-3.51	-13.74
	-0.70	599.41	-0.85	-22.68	-1.99	5.19
140	-3.26	1776.83	13.24	16.45	-2.76	-56.18
	-2.41	1798.87	15.24	362.94	-9.93	-54.90
	-2.33	2819.58	40.67	193.84	-0.77	-48.62
680	-4.32	1283.23	11.08	-238.66	-3.37	-10.52
	-5.04	1356.21	19.59	-120.99	0.18	6.75
	-4.45	1232.46	17.25	-158.03	-3.08	-13.49
345	-0.53	437.34	13.40	92.78	-0.65	1.02
	-0.54	329.21	9.32	-2.08	-0.45	-2.68
	-0.81	481.38	6.20	25.01	3.40	3.25
235	-0.86	363.63	-0.37	-24.75	-1.39	-16.58
	-0.63	457.30	5.90	132.52	-2.09	-14.16
	-0.52	314.54	0.56	-26.89	-1.71	-16.37

Table S2.2: Replicate values of abiotic parameters measured in the overlying bottom water and at the sediment surface used as environmental variables tested to explain the distribution of the benthic fluxes. Dissolved oxygen (DBO), porosity, Mn- and Fe-oxide contents, stable isotope signature of the surficial organic matter, and pigment contents are presented. Sinking POC estimated at the bottom of the water column by Forest et al. (2012)

Malina Label	DBO μM	Porosity	Mn_{HCl} μmol/g	Fe_{HCl} μmol/g	$\delta^{15}N_{tot}$ ‰	$\delta^{13}C_{org}$ ‰	Chl *a* μg/g	Phaeo μg/g	POC fluxes
390	270	0.87	6.1	337.78	4.72	-26.22	n.d.	n.d.	3441.1
	271	0.86	3.94	347.38	3.96	-26.11	3.81	9.15	
	272	0.89	8.63	363.67	5.45	-26.04	3.89	10.91	
690	308	0.83	19.13	315.82	3.79	-26.57	1.11	5.13	1465.3
	308	0.82	22.52	322.47	7.15	-26.55	1.23	7.23	
	308	0.80	10.31	324.31	4.72	-25.96	1.68	5.73	
260	311	0.78	2.49	264.04	5.32	-25.39	1.23	11.37	734.3
	311	0.78	2.75	246.73	7.01	-25.55	1.03	6.05	
	311	0.78	n.d.	208.47	5.45	-25.75	1.43	8.18	
110	273	0.81	85.09	355.27	6.74	-24.00	0.13	3.56	20.5
	273	0.83	n.d.	355.46	7.81	-24.45	0.09	2.92	
	273	0.85	88.56	355.27	7.12	-24.08	0.15	4.63	
140	282	0.82	n.d.	309.17	5.54	-25.27	0.86	6.31	49.8
	282	0.86	36.81	408.35	6.49	-25.39	1.36	10.81	
	282	0.87	1 .02	427.64	6.00	-25.22	0.90	10.70	
680	303	0.80	3.42	312.42	4.42	-26.41	2.95	9.25	619.2
	303	0.76	3.32	318.53	3.86	-25.96	1.99	7.29	
	303	0.73	8.76	294.95	4.55	-25.49	1.67	6.28	
345	299	0.81	48.72	334.90	5.77	-25.12	0.04	1.27	17.8
	300	0.76	59.84	324.99	5.66	-24.55	0.08	2.24	
	301	0.81	47.83	347.42	5.76	-25.36	0.03	1.87	
235	298	0.80	64.85	303.59	5.63	-27.37	0.52	8.89	28.3
	298	0.80	61.89	323.67	5.68	-24.89	0.07	1.87	
	298	0.85	59.29	328.23	5.77	-24.72	0.02	1.71	

CHAPITRE 3
HOTSPOTS IN THE COLD - A PERSPECTIVE FROM BENTHIC REMINERALISATION IN THE CANADIAN ARCTIC

RÉSUMÉ DU TROISIÈME ARTICLE

Climate change and anthropogenic disturbance will affect the remote ecosystems of the Arctic Ocean. Protecting hotspots of the marine ecosystem can help to maintain its health. To reflect not only diversity but also the functioning of the ecosystem, a description of hotspots should include measures of function. In the Canadian marine Arctic, the remineralisation of nutrients at the seafloor presents a benthic ecosystem function that affects the overall marine biogeochemical cycles. Only recently, benthic remineralisation other than oxygen fluxes across the Canadian Arctic shelves has been quantified, reported and discussed in a number of publications on different regions and aspects of the Canadian marine Arctic. Here, we present an overview of the complete dataset of multiple benthic boundary fluxes and discuss its relevance concerning the following questions: (1) Where were the highest benthic fluxes were found? (2) Which regions are significantly different from other regions within the Canadian Arctic, based on multiple benthic fluxes? (3) Are benthic function hotspots general hotspots? (4) How can benthic remineralisation fluxes be used in ecological assessment? While highest fluxes were found on the shallow Mackenzie Shelf, in Lancaster Sound and the North Water Polynya, these were also significantly different from other sites. Consequently, they present benthic remineralisation hotspots, but not all primary production hotspots where found to be benthic hotspots. The collaboration with Fisheries and Oceans Canada lead to the successful integration of benthic ecosystem functions into the definition of Ecologically and Biologically Significant Areas (EBSAs),

using established criteria of EBSA assessment. Our results show, that the integration of benthic remineralisation data into larger ecosystem models and assessments is possible and can thus improve long-term marine spatial planning and protect some hotspots of our most remote marine ecosystem.

This short note was co-authored by myself, Prof. Philippe Archambault and Prof. Dieter Piepenburg. It presents a synthesis of benthic remineralisation data that has been published and discussed in subsets in the following publications:

Darnis, G., Robert, D., Pomerleau, C., Link, H., Archambault, P., Nelson, R., Geoffroy, M., Tremblay, J.-É., Lovejoy, C., Ferguson, S., Hunt, B., and Fortier, L. (2012): Current state and trends in Canadian Arctic marine ecosystems: II. Heterotrophic food web, pelagic-benthic coupling, and biodiversity, Climatic Change, 1-27, doi: 10.1007/s10584-012-0483-8

Kenchington, E., Link, H., Roy, V., Archambault, P., Siferd, T., Treble, M., and Wareham, V. (2011): Identification of Mega- and Macrobenthic Ecologically and Biologically Significant Areas (EBSAs) in the Western, Central and Eastern Canadian Arctic, Department of Fisheries and Oceans Canada, Res. Doc. 2011/XXX. iv

Link, H., Chaillou, G., Forest, A., Piepenburg, D., Archambault, P. (in press): Multivariate benthic ecosystem functioning in the Arctic - Benthic fluxes explained by environmental parameters in the southeastern Beaufort Sea, Biogeosciences Discussion

Link, H., Piepenburg, D., Archambault, P. (chapitre 4): Are hotspots always hotspots? Temporal variability and its role for the relationship between diversity and ecosystem functioning in Arctic benthic environments

As first author, I conducted the experimental work, the laboratory and statistical analyses and wrote the publication. I also wrote all parts concerning benthic remineralisation in the publications listed above. Prof. Philippe Archambault contributed to the original idea and contributed to the writing. Prof. Dieter Piepenburg participated in the production of the manuscript. I have presented parts and short versions of this publication at the following conferences: (1) *CHONe Network Meeting* in Montreal (Canada) in October 2009 (2) *Forum québecois en sciences de la mer* in Rimouski (Canada) in November 2009 (3) *ArcticNet Annual Scientific Meeting* in Victoria (Canada) in December 2009 (4) *Fisheries and Oceans Science Advice Meeting* in Winnipeg (Canada) in June 2011 and (5) *IPY 2012 - From Knowledge to Action* in Montreal (Canada) in April 2012.

HOTSPOTS IN THE COLD – A PERSPECTIVE FROM BENTHIC REMINERALISATION IN THE CANADIAN ARCTIC

Introduction

Climate change and anthropogenic disturbance will affect the still remote ecosystems of the Arctic Ocean. Protecting hotspots of the marine ecosystem can help to maintain its health. In the common understanding, hotspots are considered sites or regions with higher properties (such as biodiversity) than the average.

One of the targets formulated in the Convention on Biological Diversity Strategic Plan 2011-2020 is the description of ecological and biological significant areas (EBSAs). Description of EBSAs shall provide a baseline for stakeholders, which will help to prioritize the protection of ecologically more important regions in the face of continuing economic development. To define EBSAs, the Department of Fisheries and Oceans Canada has developed Criterias and Dimensions that can be used to assess the level of different ecosystem features (e.g. feeding, biodiversity; DFO, 2004). The definition of EBSAs includes hotspots of biodiversity, and descriptions of the latter will therefore likely receive increasing attention in the next years.

Hotspots of ecosystems are often described based on a high biodiversity encountered in an area (Myers et al., 2000). This assumes that high biodiversity equals elevated ecosystem functioning, services of the area to the surrounding ecosystem (Yachi and Loreau, 1999). But there is evidence of high variability in biodiversity-ecosystem function relationships, depending on the system and scale that are considered (Stachowicz et al., 2007). We therefore believe it important to integrate ecosystem functions in the description of biological hotspots.

Biological productivity is often used as a measure ecosystem functions (Danovaro et al., 2008). In benthic environments, the remineralisation of detritus and release of inorganic nutrients back into the water column are other important processes for the functioning of

marine ecosystems. These nutrients are part of the global marine biogeochemical cycles and ultimately determine primary production in surface waters. The level of benthic remineralisation also influences the oxygenation state of sediments, which strongly influences the suitability of benthic habitats for different species (Rosenberg et al., 2001).

Knowledge of benthic processes in the Canadian Arctic has increased notably since the late 1990ies. Data on benthic carbon remineralisation on the Beaufort Shelf has been published from the Canadian Arctic Shelf Exchange Study (CASES, 2003-2004) (Renaud et al., 2007a;b) and the North Water Polynya study (NOW, 1997-1998, Grant et al., 2002) in northern Baffin Bay, but the region is still under-studied compared to other parts of the Arctic (Klages et al., 2004; Wassmann et al., 2011). Results from studies on benthic remineralisation in Canadian Arctic in 2008-2009 have recently been published in different places (Kenchington et al., 2011; Darnis et al., 2012). The aim of this paper is to compile and give a comprehensive overview of results on multiple benthic boundary fluxes in the Canadian Arctic with emphasis on describing hotspots based on benthic remineralisation function. We discuss our findings in relation to earlier results and their potential in integrative applied studies.

Origin of data and statistical analyses

Since 2008, we collected data on fluxes at the sediment-water interface including respiration and for the first time also nutrient release (phosphate, silicic acid, nitrate, nitrite and ammonium) at 42 sites in the Canadian Arctic (Fig. 3.1, Table 3.1). We ran ship-based temperature and light-controlled microcosm incubations of samples from the Mackenzie Shelf, the Amundsen Gulf and Viscount-Melville Sound in 2009, and from Barrow Strait, Lancaster Sound, the NOW and central Baffin Bay in 2008 and 2009. Most results and methods have been published as parts of larger-scale ecosystem studies, either from the perspective of pelagic-benthic coupling (Forest et al., 2011; Tremblay et al., 2011; Fortier et al., 2012), as analysis of environmental factors controlling benthic fluxes (Link et al., in press, chapitre 2; Link et al., chapitre 4) or contributing to a description of benthic biology

across the Canadian Arctic (Kenchington et al., 2011; Darnis et al., 2012; Fortier et al., 2012). A detailed description of methods can be found in Link et al. (in press, chapitre 2).

Table 3.1: Station list. Original station label from expedition, date of sampling, ecoregion (based on Spalding et al., 2007), region (used in statistical tests), depth [m], geographic position (Lat [°N], Long [°W],) expedition leg (Exp) and references (Ref), where and if data on benthic boundary fluxes has been published. Multiple benthic nutrient fluxes were acquired from all these sites. AG = Amundsen Gulf; AG-B = Amundsen Gulf bays including Cape Bathurst Polynya; B = Beaufort; BB = Baffin Bay; DS = Davis Strait; GF = Gibbs Fjord; LS = Lancaster Sound; MD = shallow Mackenzie Shelf; MS = Mackenzie Shelf and Slope; NOW = North Water Polynya; VMS = Viscount Melville Sound. A = ArcticNet expedition, I = IPY Circumpolar Flaw Lead Study, M = Malina Project.

Station	Date	Ecoregion	Region	Depth	Lat	Long	Exp	Ref
405B	10.06.08	B-AG-VMS	AG	546	70.667	123.01	I 9	a b c d
1116	14.06.08	B-AG-VMS	AG-B	230	70.042	126.277	I 9	a b c d
FB3	16.06.08	B-AG-VMS	AG-B	97	69.968	125.862	I 9	a b c d
DB01	19.06.08	B-AG-VMS	AG-B	95	69.827	123.604	I 9	b c d
1216	23.06.08	B-AG-VMS	AG-B	151	70.615	127.616	I 9	b c d
1200	27.06.08	B-AG-VMS	AG	207	71.532	124.297	I 9	b c d
434	30.06.08	Beaufort Sea	MD	45	70.177	133.537	I 9	b c d e
435	02.07.08	Beaufort Sea	MS	318	71.072	133.876	I 9	b c d e
9002	07.07.08	Beaufort Sea	MS	219	74.298	125.376	I 9	b c
D34	13.07.08	B-AG-VMS	AG	186	71.07	121.823	I 9	a b c d
405-10A	21.07.08	B-AG-VMS	AG	596	70.707	122.939	I 10	a b c d e
408-10A	25.07.08	B-AG-VMS	AG	206	71.323	127.606	I 10	b c d e
1020A	27.07.08	B-AG-VMS	AG	245	71.028	127.088	I 10	a b c d
D37 (2011-10A)	02.08.08	B-AG-VMS	AG	251	71.318	124.595	I 10	a b c d
Barrow Strait	06.09.08	LS	LS	353	74.271	91.248	A08	b c e
301	08.09.08	LS	LS	707	74.153	83.209	A08	b c e
136	10.09.08	BB-DS	BB	795	74.786	73.633	A08	b c e
140	11.09.08	BB-DS	BB	286	75.028	64.477	A08	b c
115	13.09.08	BB-DS	NOW	668	76.326	71.215	A08	b c e
108	14.09.08	BB-DS	NOW	444	76.27	74.594	A08	b c e
101	15.09.08	BB-DS	NOW	402	76.401	77.492	A08	b c
205	17.09.08	BB-DS	NOW	623	77.219	78.981	A08	b c
126	18.09.08	BB-DS	NOW	323	77.343	73.441	A08	b c
233	20.09.08	BB-DS	NOW	696	76.739	71.844	A08	b c

Table 3.1 continued

Station	Date	Ecoregion	Region	Depth	Lat	Long	Exp	Ref
Gibbs fjord 2	24.09.08	BB-DS	GF	452	70.768	72.264	A08	b c
390	31.07.09	Beaufort Sea	MD	47	70.178	133.569	M	c e f
690	01.08.09	Beaufort Sea	MD	55	69.486	137.942	M	c f
260	04.08.09	Beaufort Sea	MS	60	71.269	130.613	M	c f
110	06.08.09	B-AG-VMS	AG	400	71.696	126.477	M	c f
140	07.08.09	B-AG-VMS	AG	154	71.285	127.783	M	c e f
680	10.08.09	Beaufort Sea	MD	125	69.611	138.235	M	c f
345	16.08.09	Beaufort Sea	MS	577	71.382	132.652	M	c e f
235	22.08.09	Beaufort Sea	MS	576	71.764	130.766	M	c f
408	13.10.09	B-AG-VMS	AG	152	71.286	127.782	A09	c
437	14.10.09	B-A-VMS	AG	320	71.779	126.477	A09	c
405	16.10.09	B-A-VMS	AG	559	70.665	122.996	A09	c e
308	19.10.09	B-A-VMS	VMS	541	74.101	108.836	A09	c
304	23.10.09	LS	LS	331	74.318	91.406	A09	c e
323	25.10.09	LS	LS	786	74.172	80.726	A09	c e
109	28.10.09	BB-DS	NOW	451	76.29	74.137	A09	c e
115	29.10.09	BB-DS	NOW	669	76.335	71.238	A09	c e
136	30.10.09	BB-DS	NOW	810	74.687	73.349	A09	c e

a = Link et al., 2011 (O_2); b = Darnis et al., 2012 (O_2, $Si(OH)_4$, PO_4^{2-}); c = Kenchington et al., 2011 (O_2, $Si(OH)_4$, PO_4^{2-}); d = Tremblay et al., 2011 (O_2); e = Link et al., chapitre 4 (O_2, NO_3^-, NO_2^-, $Si(OH)_4$, PO_4^{2-}); f = Link et al., in press, chapitre 2 (O_2, NO_3^-, NO_2^-, NH_4^+, $Si(OH)_4$, PO_4^{2-}).

We used a 2-factor PERMANOVA design to test for differences among regions in benthic boundary fluxes. The factors 'year' (two levels: 2008, 2009), fully crossed with 'region' (seven levels: AG, BB, BS=Barrow Strait, LS, MD, MS, NOW) and their interactions were tested. The resemblance matrices quantifying the between-replicate similarities in terms of three standardized fluxes (O_2, $Si(OH)_4$, PO_4^{2-}) were calculated based on Euclidean distances. GF and VMS were excluded from the analysis due to their singular character Missing data points were replaced using the 'missing' function in PRIMER-E software. PERMANOVA pair-wise tests were run for significant sources of variation between the factors (Anderson et al., 2008).

Benthic remineralisation function in the Canadian Arctic in 2008-2009

We recorded highest oxygen fluxes from the Mackenzie Delta and Barrow Strait/Lancaster Sound (red colours, Fig. 3.1). Slightly lower fluxes were measured in the NOW and Cape Bathurst Polynya area, and lowest oxygen uptake in the central Amundsen Gulf, Viscount- Melville Sound and central Baffin Bay (green colours, Fig. 3.1). Remineralisation of sicilic acid was higher in Barrow Strait/Lancaster Sound and the NOW than in the western Canadian Arctic. Phosphate fluxes were more heterogeneous and did not show general patterns. Nitrate release was highest in the Amundsen Gulf (including bays) and on the deeper Mackenzie Shelf, while mostly uptake was measured on the shallow Mackenzie shelf and in the NOW and Lancaster Sound. At some sites, nitrate uptake was reported from one year and nitrate release in the other year (Fig. 3.1). Benthic boundary fluxes were generally lower in 2009 than in 2008 (Fig. 3.1, Kenchington et al., 2011; Link et al., chapitre 4).

The results of multivariate statistical analyses (PERMANOVA) revealed significant differences between regions based on oxygen, silicic acid and phosphate fluxes (Table 3.2, Kenchington et al., 2011). Pair-wise tests showed that benthic fluxes (a) on the shallow Mackenzie Shelf (including bays of the Amundsen Gulf) were significantly different from the Amundsen Gulf, central Baffin Bay and NOW; (b) in the NOW were significantly different from the Amundsen Gulf, central Baffin Bay and shallow Mackenzie Shelf; and (c) in Barrow Strait were significantly different from the Amundsen Gulf, central Baffin Bay, eastern Lancaster Sound and the deeper Mackenzie Shelf ('Basin') (Figure 3.2, Table 3.2, Kenchington et al., 2011). These regional differences were found despite the observed variability among sites within regions.

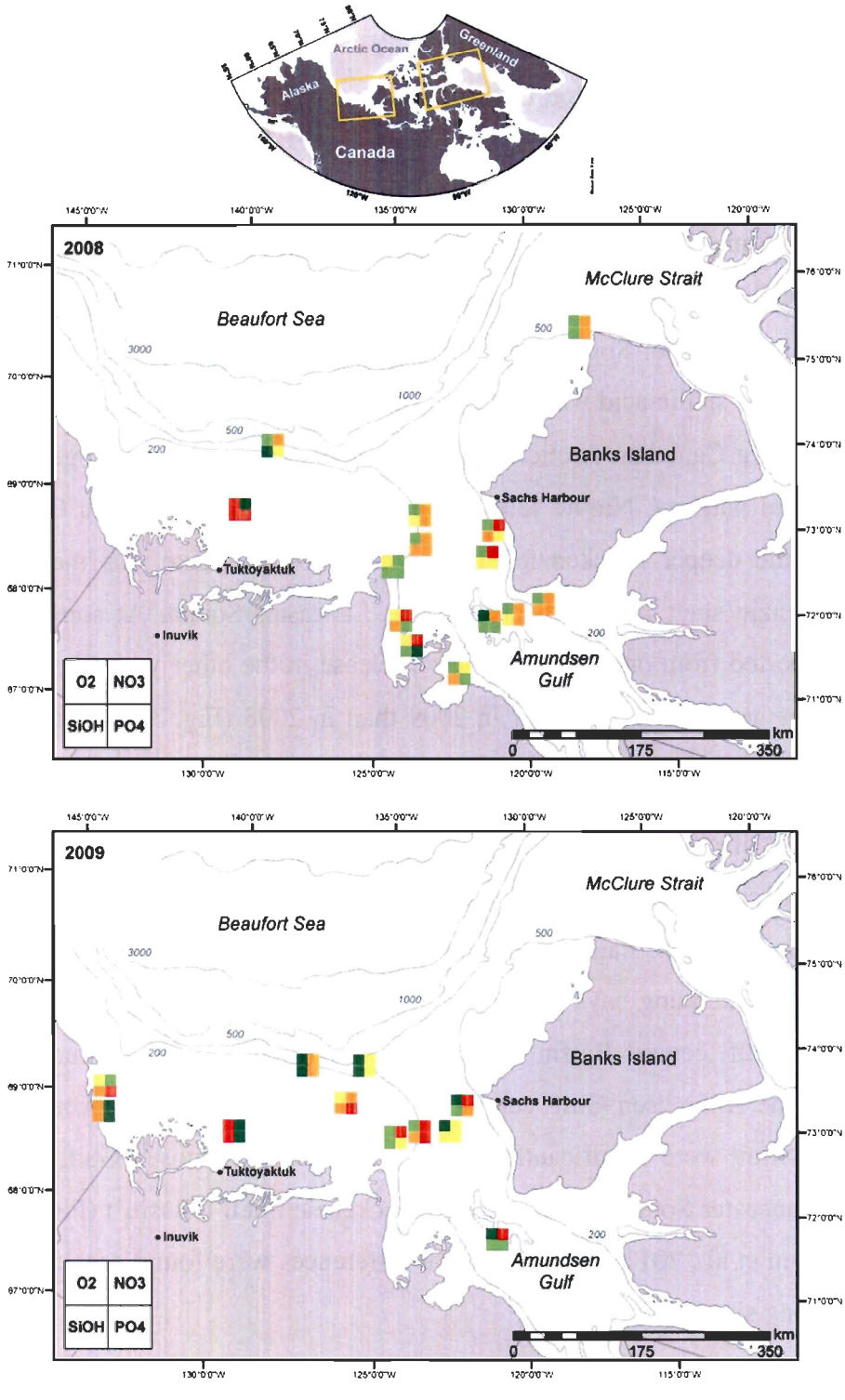
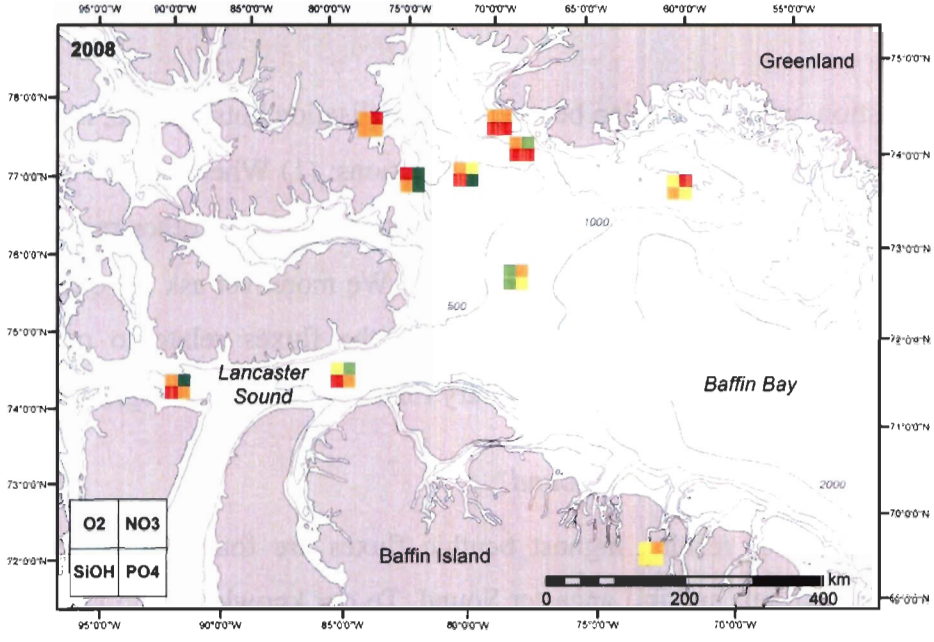
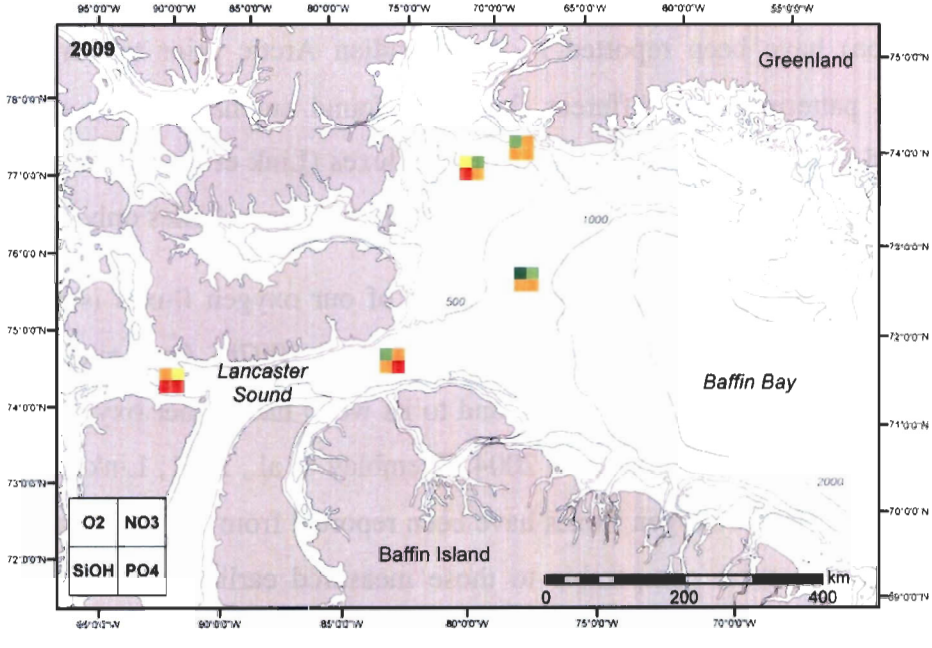


Fig. 3.1: Benthic remineralisation in the Canadian Arctic in 2008 and 2009. Fluxes from the sediment to the water column of oxygen (O2), nitrate (NO3), silicic acid (SiOH) and phosphate (PO4) are presented. Left side: southeastern Beaufort Sea; right side: Lancaster Sound, NOW and Baffin Bay; top: 2008; bottom: 2009. Modified after data published in Kenchington et al. (2011) and Darnis et al. (2012). See legend for rates and color codings





Legend

O2 (mmol m-2 d-1)	NO3 (umol m-2 d-1)	PO4 (umol m-2 d-1)	SIOH (umol m-2 d-1)
-0.99 – 0	-600 – -200	< -10	≤ 500
-2.99 – -1	-199 – -50	-10 – 0	501 – 750
-4.99 – -3	-49 – 0	0.001 – 5	751 – 1000
-9.99 – -5	1 – 100	5.001 – 15	1001 – 2000
-20 – -10	101 – 375	> 15	2001 – 6000

Canadian benthic remineralisation hotspots and what they can tell us

The question, where Canadian benthic remineralisation hotspots are, is answered by a combination of answers on the following two questions: (1) Where are the highest benthic fluxes found? (2) Which regions are significantly different from other regions within the Canadian Arctic, based on multiple benthic fluxes? We moreover ask the questions (3) Are benthic function hotspots general hotspots (how the fluxes relate to other biological parameters)? and (4) How can benthic boundary fluxes be used in ecological assessment?

Where are the highest benthic fluxes found?

According to our results, highest benthic fluxes are found in the NOW, on the shallow Mackenzie Shelf and in Lancaster Sound. To our knowledge, no benthic boundary fluxes other than oxygen (and oxygen flux translated into carbon demand or remineralisation) have been reported in the Canadian Arctic prior to our studies. The heterogeneous pattern of the different fluxes we found emphasises that oxygen fluxes cannot be used as a good proxy for other benthic fluxes (Link et al., in press, chapitre 2.). Therefore, comparison of earlier and our results apply to oxygen fluxes only.

In the southeastern Beaufort Sea, the range of our oxygen fluxes is comparable to values reported from the CASES program (Renaud et al., 2007b). Only sites closest to the Mackenzie River plume (off Tuktoyaktuk and to its west) had higher oxygen uptake (2 to 4-fold) in our study years compared to 2004 (Tremblay et al., 2011; Link et al., in press, chapitre 2). In the NOW, oxygen fluxes have been reported from 1998 (Grant et al., 2002). In 2009, our values were comparable to those measured earlier, but in 2008 they had increased to the double (Darnis et al., 2012; Link et al., chapitre 4).

While these findings allow an approximate comparison of oxygen fluxes among regions, they also stress the influence of temporal variability on flux measures in Arctic seas (Link et al., 2011; chapitre 4.). Such variability can be caused by stochastic events like an upwelling (Tremblay et al., 2011), but also by progressive changes in primary production or environmental conditions (Arrigo et al., 2008; Grebmeier, 2012).

Consequently, hotspots should not be described as steady-state regional patterns in the Arctic if results are based on single sampling events.

Where is benthic remineralisation higher and significantly different from other regions within the Canadian Arctic - and thus a hotspot?

For the two years of our study we observed that the shallow Mackenzie Shelf, the Lancaster Sound (including Barrow Strait) and the NOW were hotspots of benthic boundary fluxes. Combining the information from Fig. 3.1 and 3.2 and Table 3.2, we conclude that fluxes were significantly higher in these regions than in the Amundsen Gulf and Baffin Basin. If data from only 2008 was considered, we found similar patterns, although data from the shallow Mackenzie Shelf and bays was not sufficient to be separated from the slope and did thus not show generally high values (Darnis et al., 2012). Fig. 3.2 also shows that variability among samples in hotspot regions is higher than in other regions. The significance of the PERMANOVA test for the factor region can therefore be an effect of location of samples in the non-metric ordination or an effect of their dispersion (Anderson et al., 2008). Such variability can be caused by the differences among sites within region. But in any case, hotspot regions show a different pattern of benthic boundary fluxes than the other regions. Our dataset comprises 42 sites over two years. While we can draw conclusions with some degree of confidence for the southeastern Beaufort Sea and NOW, many regions remain understudied (Kenchington et al., 2011). The studies compiled here present the first benthic nutrient remineralisation data in the Canadian Arctic, and the overall first data in Lancaster Sound. Still, no data is available from the Canadian Arctic further north of our study area. Future surveys will be necessary to confirm current and discover further hotspots of benthic remineralisation for marine global biogeochemical budgets.

It is interesting to note that the ordination of sites in Fig. 3.2 does not follow a longitudinal gradient, and thus supports the classification of different regions in the Canadian Arctic as group of higher (hotspots) or group of lower fluxes (coldspots) (see also Link et al., chapitre 4). A similar grouping of regions in the Canadian Arctic has also been

proposed for primary production patterns of 2005-2007 (Ardyna et al., 2011), differentiating eutrophic from oligotrophic regimes. Grouping regions based on their multivariate similarity in multiple processes may be a powerful tool for understanding the functioning of ecosystems and describing hotspots on larger scales.

Table 3.2: Effects of factors on multivariate benthic fluxes and difference between regions. Results are from permutational multivariate analyses of variance (PERMANOVAs) testing the effect of Year (Ye), Region (Reg) and their interactions and results for pair-wise tests for the regions. Calculation is based on Euclidian distance for benthic boundary fluxes. Significance level at $P < 0.05$

Main test							
Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	P(MC)
Ye	1	9.598	9.598	3.4469	**0.0255**	9959	0.0235
Reg	2	24.325	12.163	4.3678	**0.0017**	9946	0.0009
YexReg	2	5.846	2.923	1.0496	0.3741	9947	0.3854
Res	101	281.240	2.785				
Total	106	318.00					

Pairwise test

Pairs:	t	P(perm)	Unique perms	P(MC)
MD, AG	4.2842	**0.0001**	9945	0.0001
MD, MS	1.4709	0.1165	9955	0.1204
MD, BS	1.6955	0.0549	9950	0.0586
MD, LS	1.2943	0.1877	9956	0.1894
MD, NOW	1.7406	**0.0308**	9960	0.0399
MD, BB	1.7159	**0.0464**	9964	0.0651
AG, MS	0.97889	0.3407	9933	0.3529
AG, BS	7.6111	**0.0001**	9954	0.0001
AG, LS	1.8588	0.0563	9942	0.0499
AG, NOW	4.8086	**0.0001**	9943	0.0001
AG, BB	1.7715	0.0632	9933	0.0616
MS, BS	15.305	**0.0001**	7693	0.0001
MS, LS	0.39543	0.7805	7692	0.7904
MS, NOW	1.5053	0.1134	9950	0.1202
MS, BB	3.6021	**0.0003**	7706	0.0013
BS, LS	3.6544	**0.0027**	8863	0.0037
BS, NOW	1.241	0.219	9949	0.2145
BS, BB	16.811	**0.002**	8672	0.0001
LS, NOW	1.1871	0.258	9967	0.2512
LS, BB	2.4349	**0.0268**	8885	0.0257
NOW, BB	2.4759	**0.007**	9954	0.007

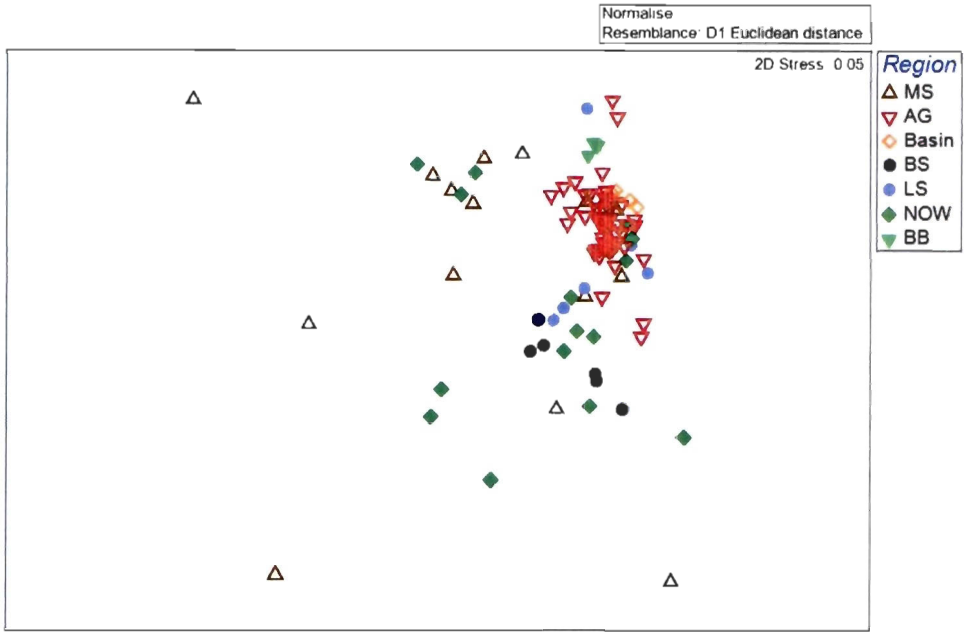


Fig. 3.2: Multidimensional Scaling Plot showing the similarity of replicates based on the three benthic fluxes of oxygen, silicic acid and phosphate. MS= (shallow) Mackenzie Shelf, AG= Amundsen Gulf, Basin= Mackenzie Basin (or Beaufort Sea), BS= Barrow Strait (western Lancaster Sound), LS= eastern Lancaster Sound, NOW= North Water Polynya, BB= Baffin Bay. Figure from Kenchington et al. (2011)

Are benthic function hotspots general hotspots?

The hotspot areas of benthic remineralisation function described (shallow Mackenzie Shelf, Lancaster Sound and NOW) are in accordance with regional patterns of benthic diversity reported elsewhere: In the NOW, both abundance and species number are high, particularly in the center of the polynya (Lalande, 2003). In Lancaster Sound, Thomson (1982) reported high macrofaunal abundance and taxonomic richness, although mostly from the shallow areas of Lancaster Sound. Recent data from the central part of Lancaster Sound also indicates high benthic diversity in terms of biomass and species number (Kenchington et al., 2011). In the southeastern Beaufort Sea, highest abundance was reported from the shallow Mackenzie Shelf and the bays of the Amundsen Gulf (Conlan et al., 2008).

General spatial patterns of primary production in the Canadian Arctic Archipelago also fit our hotspots, reporting eutrophic regimes from Lancaster Sound and the NOW. Although the recently reported hotspot of primary production in the central Amundsen Gulf (Ardyna et al., 2011) seems in contradiction to our results, marine system studies in the area confirmed high pelagic carbon cycling and low organic matter export in the central Amundsen Gulf, at least in 2008 (Forest et al., 2011). Also contrary to Ardyna et al. (2011), we found the shallow Mackenzie Shelf to be a hotspot area of benthic remineralisation. While the latter study summarizes data from 2005 to 2007, an upwelling provoked a marine system hotspot including tight pelagic-benthic coupling on the shallow Mackenzie Shelf and Amundsen Gulf bays in 2008 (Link et al., 2011, Tremblay et al., 2011). Considering a 2-fold increase of oxygen fluxes in 2009 compared to 2004 (Link et al., in press, chapitre 2), we believe that the shallow Mackenzie Shelf is a benthic remineralisation hotspot even beyond the upwelling year.

We should also note here that, although hotspots are sites with the highest fluxes, they may not be the only important regions for a global ecosystem function. Areas of particular low processes may also provide extremely rare habitats that can lead to specialized ecosystems, which are important simply due to their uniqueness.

Finally, we suggest that benthic remineralisation hotspots do reflect benthic diversity hotspots, but do not reflect primary production hotspots and can therefore not be generalized.

How can benthic remineralisation be used in ecological assessment?

Earlier and our results on benthic boundary fluxes could be integrated into the description of EBSAs in the Canadian Arctic (DFO, 2011) based on definition methods developed by the DFO (2004) and following the demand by the Convention in Biological Diversity. For this, we first defined benthic EBSAs in a larger collaborative work (Kenchington et al., 2011) including knowledge on benthic diversity, sediment pigments and coral and sponge habitats. Benthic remineralisation data could be integrated in the

dimension and criteria framework as a 'feeding' function, meaning that the release of fluxes from the sediments feeds into primary production. We present the results in Table 3.3, where High (H) values for a dimension indicate a high priority for EBSA designation, except for the Resilience dimension (low resilience equates to a higher importance for EBSA classification). A total of 20 benthic EBSAs could be defined based on biological data and supports the overall described EBSAs (Fig. 3.3), and the detailed description provides a useful tool in ecosystem management. It allows not only assessing whether a seafloor anthropogenic disturbance activity can be authorized, but also which kind would be most detrimental in which areas.

We also integrated benthic fluxes in an exercise estimating the impact of climate change on benthos in the western Canadian Arctic (Fortier et al., 2012). Based on integrative studies in the area including our data (Forest et al., 2011; Tremblay et al., 2011), we suggest the following: Predicted changes in primary production and vertical export regimes may induce a decrease in benthic fluxes (also connected to a probable decrease in benthic diversity) in the central Amundsen Gulf and on the deeper Mackenzie Shelf. In coastal areas and on the shallow Mackenzie Shelf, however, increased organic matter input could increase fluxes and lead to a reduction of sediment oxygenation on a longer time-scale. Sediments of low oxygen content are inhabited by less diverse benthic communities (Rosenberg et al., 2001). Monitoring fluxes at the sediment-water interface can thus provide a tool to survey the health of arctic soft-bottom environments, the most common habitat in the Canadian Arctic Ocean and in the oceans around the globe. However, the conclusions are based on only two years of nutrient remineralisation measurements. The impact of climate change on benthic ecosystem function should be assessed with a longer time series of data including the changes in benthic community composition.

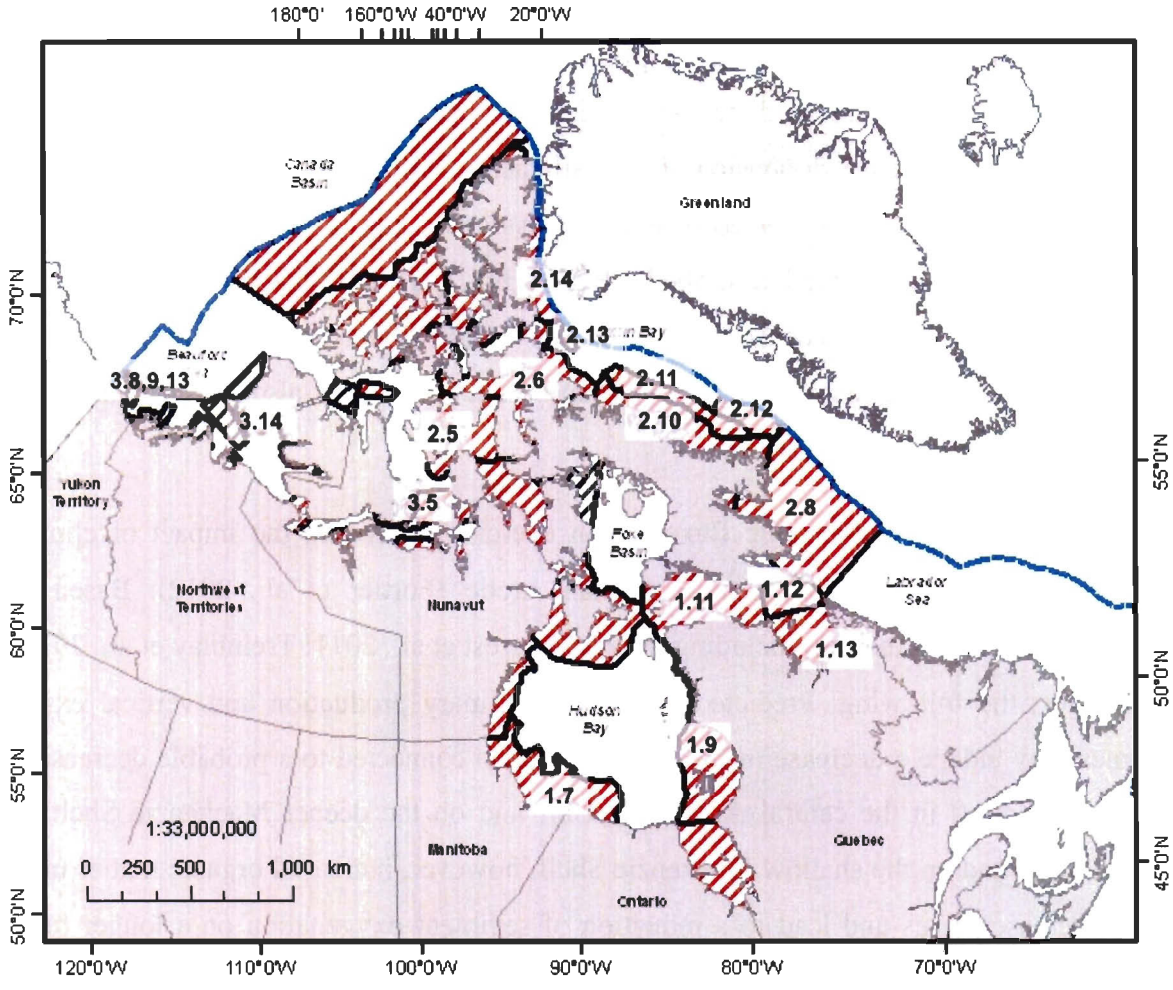


Fig. 3.3: EBSAs identified in Canadian Arctic waters by DFO (2011). Areas include those identified in 2011 (red hatch marks) and those identified previously from the northern Foxe Basin and Beaufort Sea exercises (black hatch marks). The numbers indicate EBSAs that have been confirmed with benthic data (Table 3.3). The blue dashed line represents Canada's international boundary. Modified from DFO (2011)

Table 3.3: Benthic Ecologically and Biologically Significant Areas (EBSAs) in the Canadian Arctic. An assessment of available benthic data parameters against the DFO (2004) EBSA criteria by Ecoregion, Subregion and EBSA (DFO 2011b). – Indicates insufficient data to rank; * Refers to EBSAs that were not identified by the IUCN. Table from Kenchington et al. (2011)

Ecoregion	Subregion	EBSA (DFO 2011b)	IUCN Regional EBSA / IUCN Super EBSA	Benthic Parameter	Function (F) or Structural (S) Feature	Uniqueness	Aggregation	Fitness Consequences	Resilience	Naturalness
Hudson Bay Complex		1.1 - 1.4, 1.6, 1.8, 1.10	62, 64, 65, 66			No Data to Assess				
	Southampton Island Polynya	1.5	60	Polynyas and Ice-edges	Physical Oceanographic (S)	M	H	M	-	H
	Southwestern Hudson Bay Estuaries	1.7	63	Macrobenthic Diversity	Biodiversity (S)	-	H	-	M	H
				Sediment pigment	Feeding (F)	-	H	H	-	-
	Belcher Islands	1.9	61	Macrobenthic Diversity	Biodiversity (S)	-	H	-	M	H
				Sediment pigment	Feeding (F)	-	H	H	-	-
	Hudson Strait - West	1.11	59,60	Corals and Sponges	Deep water corals (S)	M	L-M	H	H	H
				Corals and Sponges	Sponge reefs (S)	M	M	H	L	H
				Macrobenthic Diversity	Biodiversity (S)	-	H	-	M	H
				Sediment pigment	Feeding (F)	-	H	H	-	-
	Hudson Strait - East	1.12	57	Corals and Sponges	Sponge reefs (S)	M	H	H	L	H
	Ungava Bay	1.13	58	Corals and Sponges	Deep water corals (S)	M	H	H	H	H
				Corals and Sponges	Sponge reefs (S)	M	H	H	L	H
Eastern Arctic		2.1, 2.2, 2.4, 2.7	*, 67, 70, 7			No Data to Assess				
		2.9, 2.15-2.16	69, 72, 73, 6			No Data to Assess				
	Prince Regent Inlet	2.3	70, 7	Polynyas and Ice-edges	Physical Oceanographic (S)	M	H	M	-	H
	Peel Sound and Franklin Strait	2.5	71	Polynyas and Ice-edges	Physical Oceanographic (S)	M	H	M	-	H
				Macrobenthic Diversity	Biodiversity (S)	M	H	M	M	H
	Lancaster Sound and Barrow Strait	2.6	69, 70, 7	Macrobenthic Diversity	Biodiversity (S)	H	H	H	M	H
				Macrobenthic Diversity	Rare species (S)	H	L	-	-	H
				Benthic Remineralization	Feeding (F)	M	H	H	M	H
				Sediment pigment	Feeding (F)	H	H	H	L	H
				Polynyas and Ice-edges	Physical Oceanographic (S)	M	H	M	-	H
				Seabed Topography	Physical Oceanographic (S)	-	H	M	-	H
	Davis Strait and Hatton Basin	2.8	52, 57	Corals and Sponges	Deep water corals (S)	H	H	H	L	H
				Corals and Sponges	Sponge reefs (S)	H	H	H	L	H
				Corals and Sponges	Biodiversity (S)	M	H	H	L	H
	Continental Slope-Central Baffin Island	2.10, 2.11	54	Corals and Sponges	Deep water corals (S)	M	M	M	L	H
				Corals and Sponges	Sponge reefs (S)	L	L	M	L	H
				Seabed Topography	Physical Oceanographic (S)	-	H	M	-	H
	Narwhal Site and Coral Area	2.12	54	Corals and Sponges	Deep water corals (S)	H	H	H	L	H
				Corals and Sponges	Sponge reefs (S)	M	L	M	L	H
	Baffin Bay - North	2.13	69, 7	Corals and Sponges	Deep water corals (S)	H	H	H	L	H
	North Water Polynya (NOW)	2.14	69, 7	Macrobenthic Diversity	Biodiversity (S)	H	H	H	M	H
				Macrobenthic Diversity	Rare species (S)	H	L	-	-	H
				Benthic Remineralization	Feeding (F)	M	H	H	M	H
				Sediment pigment	Feeding (F)	M	H	H	L	H

Table 3.3 continued

				Polynyas and Ice-edges	Physical Oceanographic (S)	M	H	M	-	H
Western Arctic		3.1, 3.3, 3.4, 3.6				No Data to Assess				
	Bathurst Inlet	3.2	*	Polynyas and Ice-edges	Physical Oceanographic (S)	M	H	M	-	H
	West King William Island	3.5	*	Macrobenthic Diversity	Biodiversity (S)	-	H	H	-	H
				Sediment pigment	Feeding (F)	-	H	H	-	H
				Seabed Topography	Physical Oceanographic (S)	-	H	M	-	H
	Beaufort LOMA-Mackenzie Shelf	3.8, 3.9, 3.13	37, 77, 5	Macrobenthic Diversity	Biodiversity (S)	H	H	H	M	H
	Beaufort LOMA-Cape Bathurst-Amundsen Gulf	3.14	37, 76, 5	Benthic Remineralization	Feeding (F)	M	H	H	M	H
				Sediment pigment	Feeding (F)	L	M	H	L	H
	Beaufort LOMA-Franklin Bay		37	Macrobenthic Diversity	Biodiversity (S)	H	H	H	M	H
				Benthic Remineralization	Feeding (F)	M	H	H	M	H
				Sediment pigment	Feeding (F)	L	H	H	L	H
				Polynyas and Ice-edges	Physical Oceanographic (S)	M	H	M	-	H
	Beaufort LOMA-Prince of Wales Strait		*	Macrobenthic Diversity	Biodiversity (S)	-	H	H	-	H
				Sediment pigment	Feeding (F)	-	H	H	-	H
	Beaufort LOMA-Viscount Melville Sound	3.24	72, 6	Macrobenthic Diversity	Biodiversity (S)	L	L	-	L	H
				Benthic Remineralization	Feeding (F)	L	L	L	M	H
				Sediment pigment	Feeding (F)	L	L	L	-	H
Arctic Basin	Beaufort Gyre	4.1	*	Polynyas and Ice-edges	Physical Oceanographic (S)	M	H	M	-	H
High Canadian Arctic Archipelago		5.1, 5.2, 5.3, 5.4, 5.5				No Data to Assess				
			72, 6	Polynyas and Ice-edges	Physical Oceanographic (S)	M	H	M	-	H

Conclusion

Hotspot areas of enhanced nutrient remineralisation in the Canadian Arctic are reported for the shallow Mackenzie Shelf, Lancaster Sound and the NOW. They represent benthic hotspots, but are not always linked to pimary production hotspots. Further surveys of this benthic function will be necessary to confirm that the observed spatial patterns are not exceptional events of the 2008-2009 survey. Understanding the driving factors of benthic remineralisation function will help to predict shifts which climate change may cause. Integrating such data into larger ecosystem models and assessments can improve

long-term marine spatial planning and protect some hotspots of our most remote marine ecosystem.

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CHAPITRE 4

ARE HOTSPOTS ALWAYS HOTSPOTS? TEMPORAL VARIABILITY AND ITS ROLE FOR THE RELATIONSHIP BETWEEN DIVERSITY AND ECOSYSTEM FUNCTIONING IN ARCTIC BENTHIC ENVIRONMENTS

RÉSUMÉ DU QUATRIÈME ARTICLE

Ecosystem-based management often relies on proxy measures such as diversity for decisions making. However, the diversity-ecosystem function relationship has not been verified in Arctic environments, and has rarely been tested for its stability in time. We studied the temporal variability of benthic ecosystem functioning at hotspots (sites with high benthic boundary fluxes) and coldspots (sites with lower fluxes) among two years in the Canadian Arctic. Benthic remineralisation function was measured as fluxes of oxygen, silicic acid, phosphate, nitrate and nitrite at the sediment-water interface. In addition sediment pigment concentration and macrobenthic diversity (taxonomic and functional) were determined. To separate temporal from spatial variability, we sampled the same nine sites from the Mackenzie Shelf to Baffin Bay during the same season (summer or fall) in 2008 and 2009. We observed that temporal variability of benthic remineralisation function at hotspots is higher than at coldspots and that taxonomic and functional community composition does not change significantly between years. Unexpectedly, temporal variability of food availability (i.e., sediment surface pigment concentration) seemed higher at coldspots than at hotspots. Sediment chlorophyll a (Chl *a*) concentration, taxonomic richness, total abundance, water depth and abundance of the largest gallery-burrowing

polychaete *Lumbrineris tetraura* together explained 42 % of the total variation in fluxes. Food supply proxies (i.e., sediment Chl *a* and depth) split hot- from coldspot stations and explained variation on the axis of temporal variability, and macrofaunal community parameters explained variation mostly along the axis separating eastern from western sites with hot- or coldspot regime. We conclude that variability in benthic remineralisation function, food supply and diversity will react to climate change on different time scales, and that their interactive effects may hide the detection of progressive change particularly at hotspots. Time-series of benthic functions and its related parameters should be conducted at both hot- and coldspots to produce reliable predictive models.

Keywords: diversity, ecosystem functioning, Arctic, benthic remineralisation, sediment pigments, functional diversity, spatio-temporal variation, time-series

This article was co-authored by myself, Prof. Philippe Archambault and Prof. Dieter Piepenburg. As first author, I conducted the experimental work, most of the laboratory and statistical analyses and wrote the publication. Prof. Philippe Archambault contributed to the original idea and to the writing. Prof. Dieter Piepenburg participated in the production of the manuscript. The manuscript is in an early production state and is planned to be submitted to *PlosONE* by the end of 2012. I have presented parts and short versions of this publication at the following conferences: (1) *ArcticNet Annual Scientific Meeting* in Ottawa (Canada) in December 2010 (2) *Hermione Network Meeting* in Malaga (Spain) in April 2011 (3) *CHONe Network Meeting* in Montreal (Canada) in April 2011 (4) *Word Congress on Marine Biodiversity* in Aberdeen (Scotland) in September 2011 and (5) *Annual General Meeting of Québec-Océan* in Lac Délage (Canada) in November 2011.

ARE HOTSPOTS ALWAYS HOTSPOTS? TEMPORAL VARIABILITY AND ITS ROLE FOR THE RELATIONSHIP BETWEEN DIVERSITY AND ECOSYSTEM FUNCTIONS IN ARCTIC BENTHIC ENVIRONMENTS

Introduction

Can we use the diversity of communities to predict ecosystem functions? This question has been nourishing the experimental efforts and discussions of terrestrial and marine ecologist for some time (Naeem et al., 2009; 2012). But very few studies have explicitly investigated the relationship between biodiversity and ecosystem functions at higher latitudes (Schmid et al., 2009). Ecosystem functioning, defined as the biogeochemical and biotic processes and interactions in an ecosystem, is strongly related to ecosystem services providing, e.g., wood or fish for human needs (Cardinale et al., 2012). With global changes underway, such ecosystem services are threatened and, hence, efforts are increasing to define the role of biodiversity and its changes for ecosystem functions (Hooper et al., 2012). Particularly hotspots of species richness are considered an insurance of functioning in the face of species loss. Other studies have demonstrated the importance of resource availability modifying the diversity- ecosystem function relationship (Fridley, 2002; Godbold and Solan 2009; Wahl et al., 2011).

Polar ecosystems are of particular interest, because climate changes are affecting them faster and stronger than the ecosystems in other regions (Doney et al., 2012). There is thus a need for particularly rapid assessment of how environmental changes may alter ecosystem functioning in polar latitudes. In contrast to most other oceans, more than half of the Arctic Ocean's total area consists of rather shallow continental shelves. Understanding shelf-environments is indispensible for a description of the marine Arctic ecosystems and their functioning. While recent reviews have achieved an inventory of benthic diversity of Canadian and pan-Arctic shelves (Cusson et al., 2007; Piepenburg et al., 2011), their benthic ecosystem functioning is understudied (Wassmann et al., 2011). In soft-bottom environments, which dominate Arctic continental shelves, the degradation of organic

matter and coupled oxygen and inorganic nutrient fluxes from the sediments back to water column is an important ecosystem function (Emmerson et al., 2001). Benthic oxygen consumption is generally linked to the availability of food resources, which are often measured as sediment pigments (Clough et al., 2005; Grebmeier et al., 2006b; Renaud et al., 2007a). Knowledge on the remineralisation of other nutrients from the sediments in the Canadian Arctic has only recently been reported (Darnis et al., 2012), and is not directly correlated to oxygen fluxes (Robert et al., 2012, Link et al., in press, chapitre 2). This underlines the need to investigate, which factors influence benthic remineralisation function as a whole. In other habitats and experimental studies for example, the role of the number and identity of species for oxygen consumption and nutrient fluxes at the sediment-water interface have been clearly demonstrated (Ieno et al., 2006; Michaud et al., 2006; Piot, 2012). Moreover, the functional diversity seems to be more important than number of taxa (Harvey et al., 2012).

At sites with higher benthic remineralisation than known on average from the Canadian Arctic (Kenchington et al., 2011; Darnis et al., 2012), which we define as **hotspots**, we have recently found high temporal variability of oxygen consumption. But sites characterized by a generally low oxygen consumption (hereafter '**coldspots**') showed lower temporal variability (Link et al., 2011; Forest et al., 2011; Tremblay et al., 2011). Time-series data from deep-sea sites also report important interannual variability of the downward export of organic matter (Baldwin et al., 1998), but changes in macrofaunal benthic community composition are observed only after several years or decades (Grebmeier, 2012). While temporal and regional variabilities in benthic oxygen uptake in the Arctic have so far been linked to environmental factors and food supply, it is not clear to which extent the benthic diversity affects multiple benthic fluxes (Glud et al., 2000; Schmid et al., 2009).

For most areas of the Arctic, predictive models have to rely on few benthic data collected from different locations at different times, because Arctic time-series studies are even rarer than in other oceans (Glover et al., 2010; Soltwedel et al., 2005). But the use of

such datasets to detect directional (progressive) change can be affected by the natural variability (stochastic change) of marine systems (Glover et al., 2010). Climate forced environmental changes introduce additional temporal and spatial variability of ecosystem functioning. Here we assess how diversity (taxonomic and functional; composition, species number and abundance) and environmental factors affect spatial *vs* temporal variability of ecosystem functions at hotspots and coldspots in the Canadian Arctic. The objectives of this study were to distinguish between the temporal and spatial variation in a multivariate benthic ecosystem function in the Canadian Arctic, and to investigate the relation of the often used function proxies diversity and food supply with spatio-temporal variation. The resampling of study sites in the same season of different years for multiple remineralisation fluxes, diversity and sediment pigments was the key approach to allow for separating temporal from spatial variation in the diversity-ecosystem function analysis.

We test specifically the following hypotheses: (1) Benthic remineralisation function is significantly different among years at hotspots but not at coldspots, (2) food availability for the benthos (measured as sediment pigments) is significantly different among years at hotspots but not at coldspots, (3) Taxonomic community composition is not significantly different among years, (4) Functional community composition is not significantly different among years, and (5) Food supply explains temporal variation and macrofaunal community parameters (e.g., total abundance, richness) explain spatial variation in benthic remineralisation functioning. The results will allow evaluating whether diversity can serve as a reliable surrogate for benthic remineralisation function in the Canadian Arctic despite temporal variability in polar ecosystem processes.

Methods

Study region

The study covered the benthic ecosystems in shelf environments across the Canadian Arctic Archipelago from the eastern Mackenzie Shelf in the west to the North Water Polynya (NOW) in Northern Baffin Bay in the east (Fig. 4.1). These environments are

characterised by strong seasonality, with the productive period being subjected to the timing of ice-melt and increasing light duration as summer arrives.

The eastern Beaufort Sea and Amundsen Gulf are dominated by coastal shelves down to 600 m water depth. Pelagic primary production ranges from 30 to 70 g C m^{-2} yr^{-1}, indicating generally oligotrophic conditions (Sakshaug, 2004). Rather low primary production was also found in summer and fall 2005-2007 in the eastern Beaufort Sea with daily production rates of 73 ± 37 mg C m^{-2} d^{-1} (Ardyna et al., 2011). In the Cape Bathurst Polynya at the eastern boundary of the Amundsen Gulf, however, annual production rates are higher than usual, reaching 90 to 175 g C m^{-2} yr^{-1} (Arrigo and van Dijken, 2004). Ardyna et al. (2011) reported daily primary production rates in summer of 159 ± 123 mg C m^{-2} d^{-1}, and intensive phytoplankton blooms related to ice-edge upwelling events were documented for coastal regions of the Mackenzie Shelf and Amundsen Gulf in 2008 (Mundy et al., 2009; Tremblay et al., 2011) Annual vertical POC fluxes of 1.6–1.8 g C m^{-2} yr^{-1} and 2.4 g C m^{-2} yr^{-1} were estimated at 200 m water depth for the Mackenzie Shelf and the Cape Bathurst Polynya, respectively (O'Brien et al, 2006; Forest et al., 2007; Lalande et al., 2009). Seafloor sediments are usually composed of more than 70 % silt and clay (Conlan et al., 2008).

The eastern North-West-Passage is marked by the opening of Lancaster Sound into Baffin Bay. From its western limitation at the Barrow Strait sill (125 m) the channel reaches a depth of more than 800 m in the sound itself. Tidal and bathymetry induced mixing of Pacific and Atlantic waters east of Barrow Strait allow for high primary production with rates of 251 ± 203 mg C m^{-2} d^{-1} (Ardyna et al., 2011) and an annual mean of about 60 g C m^{-2} yr^{-1} (Welch et al., 1992; Michel et al., 2006). Vertical export can be high (Fortier et al., 2002) and studies on benthic biomass and diversity report values that are among the highest known from the Arctic (Thomson, 1982), but important gaps of data need to be filled for a more comprehensive description of the area (McLaughlin et al., 2006; Michel et al., 2006; Piepenburg et al., 2011).

The North Water Polynya (NOW) is located in Baffin Bay north of Lancaster Sound. It opens each year depending on latent heat fluxes, ice-bridge formation and northerly winds over the Nares Strait between western Greenland and eastern Ellesmere Island (Ingram et al., 2002; Dumont et al., 2009). In general, its productivity is considered to be the highest in the Arctic with primary production reaching values up to 250 g C m^{-2} yr^{-1} in the east (Klein et al., 2002) and 150 g C m^{-2} yr^{-1} (Sakshaug, 2004; Ardyna et al., 2011). A significant amount of organic carbon is exported to water depths of > 200 m with highest values in the western polynya (Hargrave et al., 2002). The seabed under the polynya reaches a depth of around 700 m and studies on benthic carbon turnover showed comparatively low rates in 1998 (Grant et al., 2002) and higher rates in 2008 (Darnis et al., 2012). Abundance of benthic fauna was highest in the NOW center, indicating the role of currents and possible advection processes in the food supply for the benthos (Lalande, 2003).

Field sampling

Samples were collected from nine sites (MD-C, AG-CW, LS-W, LS-E, NW-C, NW-E (hotspots) and MS-C, AG-CC, BB-N (coldspots), Fig. 4.1) distributed across the study region in 2008 and 2009. To avoid confounding influence of seasons, the same sites were sampled in the same season each year. Sampling was conducted onboard the CCGS Amundsen between July and October during the Circumpolar Flaw Lead Study (Deming and Fortier, 2011), ArcticNet expeditions in collaboration with the Canadian Healthy Ocean Network (Snelgrove et al., 2012) and the Malina project (http://malina.obs-vlfr.fr/). Locations were chosen to study both hotspots and coldspots in the Canadian Arctic. A hotspot site was defined as an areas known for high primary productivity, vertical export and benthic fluxes (Mackenzie Delta plume, Cape Bathurst Polynya, Lancaster Sound, NOW) from previous knowledge. A coldspot site was defined as the opposite outside such areas, which generally show low benthic fluxes. More information on the definition and categorisation is found in Darnis et al. (2012) as well as Kenchington et al. (2011), respectively. At each sampling event ('station'), an USNEL box corer was deployed for seafloor sediment collection. From each box core, three to five sub-cores of ten cm

diameter and approximately 20 cm sediment depth were taken for assessing benthic remineralisation function (i.e., benthic oxygen demand and nutrient remineralisation) in shipboard microcosm incubations (Table 4.1). After incubation, the same sediment cores were passed through a 0.5 mm mesh sieve under slow running seawater. The sieve residues were preserved in a 4 % seawater-formaldehyde solution for later analyses of species diversity and abundance under a dissection microscope. Sediment surface (first cm) of additional three sub-cores were stored in pre-weighed plastic vials and frozen immediately at –80 °C to determine sedimentary Chl *a* and phaeopigment concentrations later in the laboratory (Table 4.1). Part of the data presented here has been published in oceanograpic descriptive here (Table 4.1, Darnis et al., 2012; Link et al., 2011; Link et al., in press, chapitre 2; Tremblay et al., 2011).

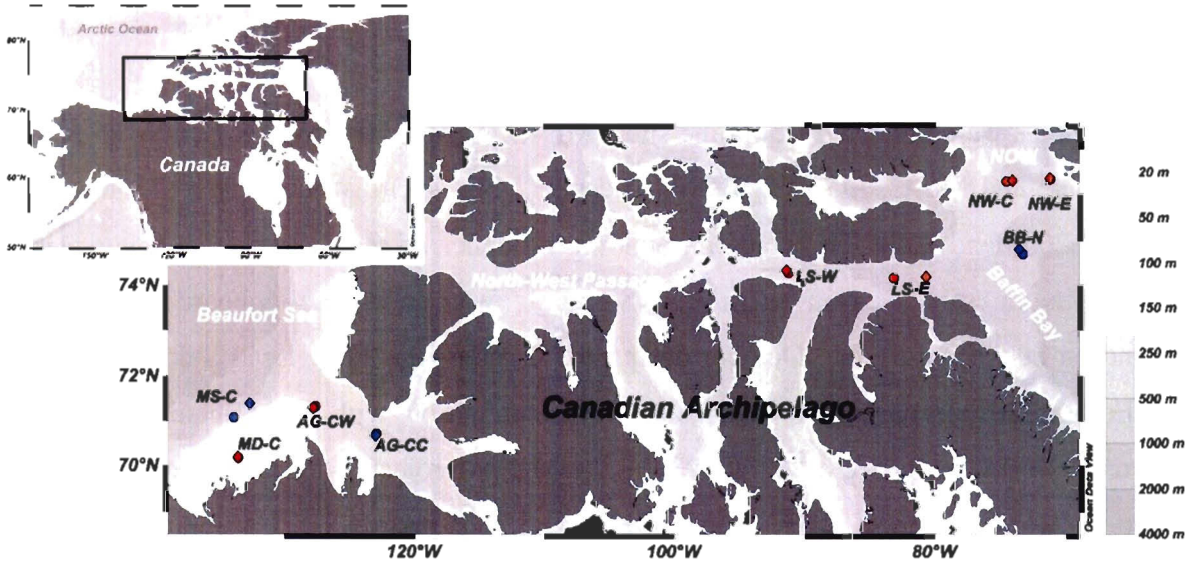

Fig 4.1: Locations of sites sampled across the Canadian Arctic in 2008 and 2009. Red = hotspots, blue = coldspots; circle = 2008, diamonds = 2009. Note that one point on the map can represent two sampling events when exact relocation was achieved

Benthic oxygen and nutrient fluxes at the sediment-water interface

Shipboard incubations of sediment microcosms were run in a dark, temperature-controlled room (2 to 4 °C) for 24 to 48 h. Total sediment oxygen flux was determined as the decrease in oxygen concentrations in the water phase and was measured periodically (2

to 8 h intervals) with a non-invasive optical probe (Fibox 3 LCD, PreSens, Regensburg, Germany). To determine changes in nutrient concentrations, samples of the overlying water phase were taken at three times during the incubation, including the onset and end.

Table 4.1: Station list. Labels, date of sampling, geographic position, number of within-station replicate samples used to determine each benthic boundary flux and diversity (BBF) and food supply proxies (sedimentary Chl a, and phaeopigments), and references (Ref), where data has been published. For sub-regions: AG = Amundsen Gulf, MD = Mackenzie Delta, MS = Mackenzie Shelf/Slope; LS = Lancaster Sound; NW = North Water Polynya; = BB = Baffin Bay; C, E, N, W = central, east, north, west; A = ArcticNet expedition, I = IPY Circumpolar Flaw Lead Study, M = Malina Project.

Regime	Site	Station label	Date	Depth [m]	Latitude [°N]	Longitude [°W]	BBF (n)	Food proxy (n)	Ref
Hotspot	MD-C	I-434	30/Jun/08	45	70.177	133.537	4	3	b c
		M-390	31/Jul/09	47	70.178	133.569	3	3	a
Hotspot	AG-CW	I-408	25/Jul/08	206	71.323	127.606	3	3	b
		M-140	07/Aug/09	154	71.285	127.783	3	3	b
Hotspot	LS-W	A-304	06/Sep/08	353	74.271	91.248	3	3	b
		A-304	23/Oct/09	331	74.318	91.406	3	3	
Hotspot	LS-E	A-301	08/Sep/08	707	74.153	83.209	3	3	b
		A-323	25/Oct/09	786	74.172	80.726	3	3	
Hotspot	NW-C	A-108	14/Sep/08	444	76.27	74.594	3	3	b
		A-109	28/Oct/09	451	76.29	74.137	3	3	
Hotspot	NW-E	A-115	13/Sep/08	668	76.326	71.215	3	3	b
		A-115	29/Oct/09	669	76.335	71.238	3	3	
Coldspot	MS-C	I-435	02/Jul/08	318	71.072	133.876	4	3	b c
		M-345	16/Aug/09	577	71.382	132.652	3	3	a
Coldspot	AG-CC	I-405	21/Jul/08	596	70.707	122.939	5	3	b c d
		A-405	16/Oct/09	559	70.665	122.996	3	3	a
Coldspot	BB-N	A-136	10/Sep/08	795	74.786	73.633	3	3	b
		A-136	30/Oct/09	810	74.687	73.349	3	3	

a = oxygen fluxes, silicic acid fluxes, phosphate fluxes and food proxy (Link et al., in press, chapitre 2); b = oxygen fluxes, silicic acid fluxes, phosphate fluxes and food proxy (Darnis et al., 2012); c = oxygen fluxes and food proxy (Tremblay et al., 2011);d = oxygen fluxes, food proxy and benthic biomass (Link et al., 2011)

Oxygen and nutrient fluxes were determined as the slope of the linear regression of the oxygen and nutrient concentration on incubation time and corrected for solute concentration in the replacement water. A more detailed description of this method can be found in Link et al. (2011) and Link et al. (in press, chapitre 2).

Sediment pigment concentration

Chl *a* and phaeopigment concentrations were analysed fluorometrically following a modified protocol proposed by Riaux-Gobin and Klein (1993) as described in Link et al. (2011). Two grams of wet substrate were incubated with 10 ml 90 % Acetone (v/v) for 24 h at 4 °C, and the supernatant was measured in a Turner Design 20 fluorometer before and after acidification. Chl *a* and total pigment concentration (Chl *a* + phaeopigments) were determined. Quantities are expressed as microgram pigment per gram of dry sediment [μg g-1].

Macrofaunal diversity

Taxonomic diversity

Sediment residues from the sieved incubation cores were sorted under a dissection microscope in the lab to retrieve benthic organisms that were subsequently identified to the lowest possible taxonomic level and counted (abundance, N). Taxa not identified to the species level were distinguished from other specimen (e.g. sp. 1) and classified as morpho-species. Where such consistency across the study region was not achieved (e.g., due to a lack of describable characters), specimens were grouped into the lowest common taxon (e.g., *Sipuncula*). Taxonomic richness is the number of taxa at each station (Tax S or S_{Tax}).

Functional diversity

Consequently, species were classified into functional groups according to their traits in terms of feeding mode, body size, mobility and bioturbation influence (Table 4.2, Table S4.1) (Bremner et al., 2003; Pearson, 2001; Petchey and Gaston, 2006). Categories were chosen based on their presumed influence on benthic remineralisation. Species were allowed more than one trait for feeding mode. Trait information was retrieved from the best

resources available (Fauchald and Jumars, 1979; Todd, 2001; MarLIN, 2006; Australian Museum, 2009; Kedra et al., 2009; MarLIN, 2009; Macdonald et al., 2010; Appeltans et al., 2012).

Table 4.2: Functional traits. Categories of traits and their levels used to define functional groups for taxa.

	Category			
	Feeding/Diet	Size	Mobility	Bioturbation
Level	C = Carnivorous (predator or passive suspension)	S < 3 mm	M = Mobile	B = Active burrower (diffusive)
	D = Surface deposit feeder	3 mm < M < 10 mm	S = Sessile	G = Gallery burrower
	F = Filter/Suspension feeder	L > 10 mm	H = Hemimobile	S = Surface dweller
	O = Omnivorous (scavenger)			T = Tube burrower
	P = Parasite			
	S = Subsurface deposit feeder			

For analyses of composition and richness, functional groups were treated in the same way as taxonomic entities. Functional group richness is the number of different categories of traits per station (S_{Func}).

Statistical analyses

We used a mixed-model PERMANOVA design to test for temporal and spatial differences in (a) benthic boundary fluxes, (b) food supply proxies (i.e., sediment pigment concentrations), (c) taxonomic and (d) functional composition. The factors 'year' (two levels: 2008, 2009), fully crossed with 'regime' (two levels: hotspot, coldspot),'sites' nested in 'regime' (six sites MD-C, AG-CW, LS-W, LS-E, NW-C, NW-E (hotspot) and three sites MS-C, AG-CC, BB-N (coldspot)) and their interactions were tested. The resemblance matrices quantifying the between-replicate similarities in terms of all five standardized fluxes (O_2 and four nutrients) and the two sediment pigments were calculated based on Euclidean distances. Missing data points were replaced using the 'missing' function in PRIMER-E software. Taxonomic and functional abundance matrices were fourth-root transformed and their resemblance matrices were calculated based on Bray-

Curtis similarity (Clarke and Gorley, 2006). PERMANOVA pair-wise tests were run for significant sources of variation between the factors (Anderson et al., 2008). The significance level was corrected for multiple testing using the Bonferoni correction with $\alpha_B = \alpha/n$, where n is the number of comparisons and $\alpha=0.05$. Homogeneity of dispersion could not be tested for groups of the interaction terms 'year x site (regime)' using the PERMDISP routine due to the small sample size (n = 3) (Anderson et al., 2008). Instead, we determined average squared distances (Euclidian, for fluxes and pigments) or dissimilarities (Bray-Curtis, for taxonomic and functional composition) across sites within and between years for samples of hotspots and coldspots, respectively, using the SIMPER routine (Clarke and Gorley, 2006). Multidimensional Scaling (MDS) plots were used to visualize the resemblance patterns.

A stepwise distance-based linear model permutation test (DistLM, McArdle and Anderson, 2001) was performed to identify which subset of biotic and environmental variables predict the multivariate variation of five benthic boundary fluxes at 18 stations (all stations of 2008-2009) best. Ten predicting variables were allowed to enter the model: sediment surface Chl *a* concentration, sediment surface phaeopigment concentration, taxonomic richness, functional group richness, abundance, Shannon-Wiener index, abundance of the largest gallery burrower *Lumbrineris tetraura* (single species of its functional group) and abundance of the largest dominant tube-burrower group DFLHT, water depth and the date of ice-free conditions. Ice-free conditions were determined from weekly ice charts for the western and eastern Canadian Arctic published by the Canadian Ice Service (CIS) available on http://www. ec.gc.ca/glaces-ice/. A site was considered to be ice-free, if ice concentrations below 1 prevailed for more than two consecutive weeks. To meet the linearity assumption for predictor variables, Chl *a* was ln transformed prior to analysis. No pair of variables was linearly correlated by $r > 0.85$ and hence all variables were retained for possible inclusion in the model. The stepwise routine was run employing 9999 permutations and using the AIC_c selection criterion. The AIC_c was devised to handle situations where the number of samples (N) is small relative to the number (v) of predictor

variables (N/v<40) (Anderson et al., 2008). Results were visualized with a distance-based redundancy analysis (dbRDA) (Anderson et al., 2008).

Results

Temporal and spatial variability of benthic boundary fluxes

In general, benthic boundary fluxes were higher at hotspots than at coldspots and higher in 2008 than in 2009 (Fig. 4.2). This pattern was most pronounced for oxygen fluxes, whereas other nutrient fluxes showed more heterogeneous patterns. Sites of greatest benthic oxygen and nitrate uptakes, and silicic acid and phosphate releases were MD-C, NW-C and LS-W (all hotspots) (Fig. 4.2).

The multivariate composition of benthic boundary fluxes was significantly different between hotspots and coldspots and among sites, with a significant interaction between years and the nested factor sites (Table 4.3). The years 2008 and 2009 were significantly different at the sites LS-W, LS-E, NW-C, NW-E and BB-N (Table 4.4, Fig. 4.3). Variability within and between years was greater at hotspots than at coldspots (Table 4.5).

Temporal and spatial variability of food supply

Sediment Chl *a* concentrations ranged from 0.04 to 32.44 $\mu g\ g^{-1}$ with highest values at the hotspot sites MD-C and LS-W and lowest values at coldspots. Sediment phaeopigment concentrations were higher at hotspots than at coldspots (Table S4.2).

Significant differences in the multivariate composition of sediment pigments were found between hotspots and coldspots and among sites, with a significant interaction between years and sites (Table 4.3). There were significant differences between 2008 and 2009 at sites AG-CW, MS-C and AG-CC (Table 4.4, Fig. 4.4). Variability within and between years was greater at hotspots than at coldspots (Table 4.5, Fig. 4.4).

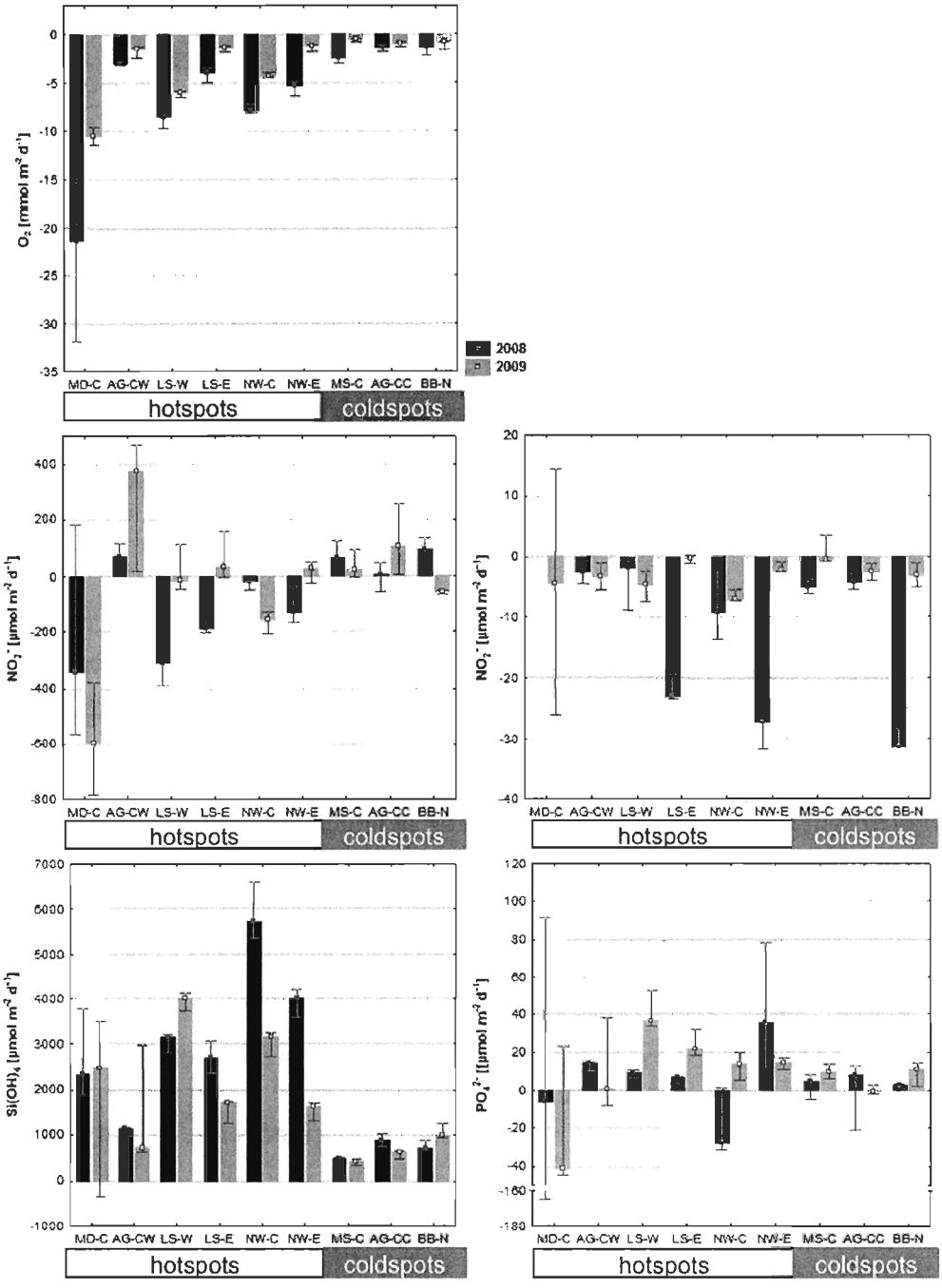

Fig 4.2: Benthic boundary fluxes at each sampling event across the Canadian Arctic in 2008 and 2009. Columns represent median ± min/max. For years: black columns = 2008, grey columns = 2009. For sub-regions: AG = Amundsen Gulf, MD = Mackenzie Delta, MS = Mackenzie Shelf/Slope; LS = Lancaster Sound; NW = North Water Polynya; = BB = Baffin Bay; C, E, N, W = central, east, north, west

Table 4.3: Effects of factors on multivariate benthic parameters. Results are from permutational multivariate analyses of variance (PERMANOVAs) testing the effect of Year (Ye), Regime (R), Site (Si) nested within Regime and their interactions. Calculation is based on Euclidian distance for benthic boundary fluxes and pigments, and on Bray-Curtis similarity of fourth-root transformed data of functional and taxonomic community composition. Significance level at $P < 0.05$

Benthic Boundary Fluxes

Source of variation	df	MS	Pseudo-F	P (perm)
Year	1	17.099	2.219	0.1047
Regime	1	43.911	3.031	0.0310
Site(R)	7	14.066	6.977	0.0001
Year x R	1	3.448	0.455	0.7892
Year x Site(R)	7	7.497	3.719	0.0001
Res	40	2.016		
Total	57			

Pigments

Source of variation	df	MS	Pseudo-F	P (perm)
Year	1	4.327	1.643	0.2436
Regime	1	36.117	8.316	0.0226
Site(R)	7	4.343	14.202	0.0001
Year x R	1	2.551	0.969	0.3643
Year x Site(R)	7	2.633	8.611	0.0001
Res	36	0.306		
Total	53			

Functional Compositions

Source of variation	df	MS	Pseudo-F	P perm)
Year	1	2056.0	1.115	0.3656
Regime	1	16579.0	3.105	0.0032
Site(R)	7	5181.4	9.496	0.0001
Year x R	1	1986.8	1.078	0.3887
Year x Site(R)	7	1801.8	3.302	0.0001
Res	40	545.6		
Total	57			

Taxonomic Diversity

Source of variation	df	MS	Pseudo-F	P (perm)
Year	1	3293.2	1.063	0.4143
Regime	1	20697.0	2.096	0.0267
Site(R)	7	9588.0	8.916	0.0001
Year x R	1	2338.5	0.758	0.6628
Year x Site(R)	7	3035.5	2.823	0.0001
Res	40	1075.4		
Total	57			

Table 4.4: Difference between years for pairs of each site based on multivariate benthic parameters. Results for PERMANOVAs pair-wise tests for the significant interaction term Year x Site (R) (Table 4.3) and the average distance between (2008 – 2009) and within (2008, 2009) groups of replicates are presented. Calculation is based on Euclidian distance for benthic boundary fluxes and pigments. Significance level after Bonferroni correction: p(MC) < 0.006. Significant results are in bold. For sub-regions: AG = Amundsen Gulf, MD = Mackenzie Delta, MS = Mackenzie Shelf/Slope; LS = Lancaster Sound; NW = North Water Polynya; = BB = Baffin Bay; C, E, N, W = central, east, north, west

Regime	Site	t	Df	P (MC)	2008 - 2009	2008	2009
	Fluxes						
Hotspots	MD-C	0.969	5	0.4221	4.86	5.33	4.09
	AG-CW	1.390	4	0.1984	1.26	0.35	1.62
	LS-W	4.184	4	**0.0043**	2.14	0.82	0.81
	LS-E	7.568	4	**0.0003**	2.79	0.52	0.67
	NW-C	3.934	4	**0.0034**	2.49	1.36	0.51
	NW-E	5.004	4	**0.0012**	3.63	1.61	0.37
Coldspots	MS-C	1.946	5	0.0631	1.12	0.95	0.50
	AG-CC	1.486	6	0.1560	0.83	0.67	0.82
	BB-N	11.942	4	**0.0003**	2.99	0.41	0.44
	Pigments						
Hotspots	MD-C	4.122	4	0.0136	3.81	2.08	0.43
	AG-CW	5.686	4	**0.0020**	0.33	0.08	0.11
	LS-W	3.350	4	0.0146	2.01	0.95	0.94
	LS-E	1.534	4	0.1939	0.70	0.41	0.73
	NW-C	0.454	4	0.6822	0.95	1.30	0.19
	NW-E	0.910	4	0.4456	0.44	0.33	0.56
Coldspots	MS-C	14.072	4	**0.0003**	0.42	0.04	0.05
	AG-CC	8.351	4	**0.0013**	0.28	0.05	0.05
	BB-N	1.328	4	0.2345	0.13	0.04	0.15

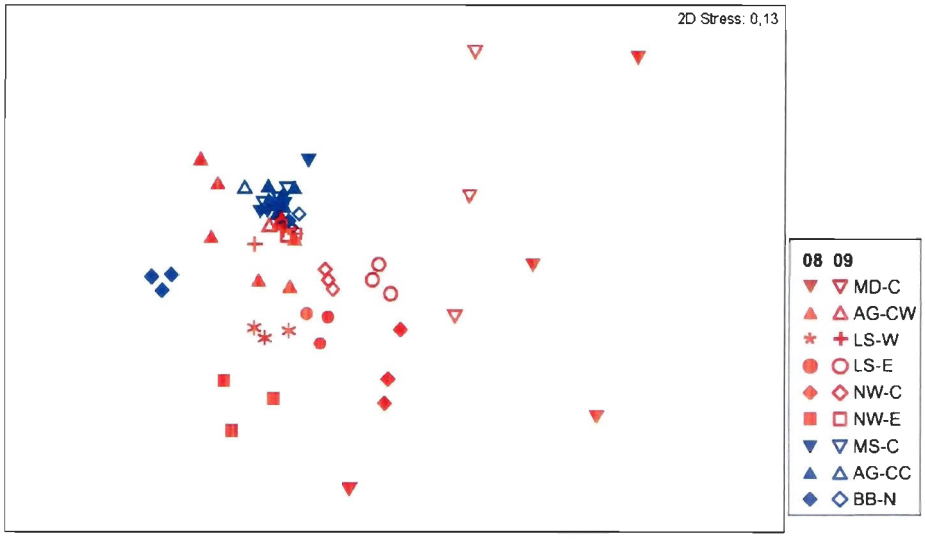

Fig 4.3: Temporal and spatial patterns of benthic boundary fluxes at each sampling event across the Canadian Arctic in 2008 and 2009. The plot shows the relative distance of samples determined as Euclidian distance of the five different fluxes. Red = hotspots, blue = coldspots; full symbols = 2008, open symbols = 2009; AG = Amundsen Gulf, MD = Mackenzie Delta, MS = Mackenzie Shelf/Slope; LS = Lancaster Sound; NW = North Water Polynya; = BB = Baffin Bay; C, E, N, W = central, east, north, west

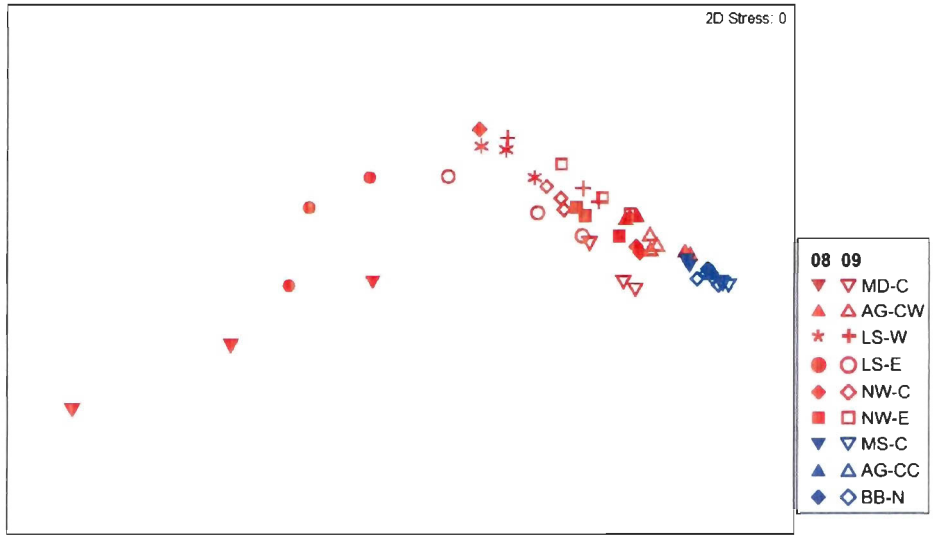

Fig 4.4: Temporal and spatial patterns of sediment pigments at each sampling event across the Canadian Arctic in 2008 and 2009. The plot shows the relative distance of samples in a 2-D space determined as Euclidian distance of Chl *a* and phaeopigments. Red = hotspots, blue = coldspots; full symbols = 2008, open symbols = 2009; AG = Amundsen Gulf, MD = Mackenzie Delta, MS = Mackenzie Shelf/Slope; LS = Lancaster Sound; NW = North Water Polynya; = BB = Baffin Bay; C, E, N, W = central, east, north, west

Table 4.5: Dispersion within and between 2008 and 2009 for hotspots and coldspots across the nested sites. Average squared distance (benthic boundary fluxes and pigments) and average squared Bray-Curtis dissimilarity calculated by SIMPER are presented

	Group	Hotspots	Coldspots
Fluxes	2008	5.08	0.34
(Sq. Eucl. Dist.)	2009	1.80	0.20
	2008 vs 2009	*10.66*	*3.08*
Pigments	2008	0.72	<0.01
(Sq. Eucl. Dist.)	2009	0.20	0.01
	2008 vs 2009	*3.73*	*0.09*
Tax. Comp	2008	44.22	50.17
(Dissimilarity)	2009	45.52	44.88
	2008 vs 2009	*57.97*	*55.57*
Func. Comp	2008	29.63	36.82
(Dissimilarity)	2009	31.07	34.86
	2008 vs 2009	*41.76*	*43.74*

Temporal and spatial variability of taxonomic diversity

We identified a total of 311 macrofaunal taxa in the sediments taken from the incubation cores (Table S4.1). Taxonomic richness (S_{Tax}) per core ranged from seven taxa at AG-CC (coldspot) up to 45 at LS-W (hotspot) (Table S4.2). Lowest abundance was found at sites MD-C and AG-CW (both hotspots) and highest in the NOW sites (hotspot) (Table S4.2).

Taxonomic composition of communities was significantly different between hotspots and coldspots and among sites, with a significant interaction between years and sites (Table 4.3, Fig. 4.5). The consecutive years 2008 and 2009 were not significantly different at any site (Table 4.6). Within-year and between-year dissimilarities of hotspot and coldspot communities were comparable (Table 4.5, Fig. 4.5).

Temporal and spatial variability of functional diversity

Taxa were classified into a total of 72 functional groups (Table S4.1). Number of functional groups (S_{Func}) per core ranged between six groups at AG-CC (coldspot) and 32 at LS-W (hotspot) (Table S4.2).

Functional composition of communities was significantly different between hotspots and coldspots and among sites, with a significant interaction between years and the nested factor sites (Table 4.3). The two years 2008 and 2009 were not significantly different at any site (Table 4.6, Fig. 4.6). Dissimilarity within years was greater across coldspots than across hotspots and comparable in 2008 and 2009 (Table 4.5, Fig. 4.6).

Table 4.6: Difference between years for pairs of each site based on multivariate benthic parameters. Results for PERMANOVAs pair-wise tests for the significant interaction term Year x Site(R) (Table 4.3) and the average similarity [%] between (2008 – 2009) and within (2008, 2009) groups of replicates are presented. Calculation is based on Bray-Curtis similarity of fourth-root transformed data of functional and taxonomic community composition. Significance level after Bonferroni correction: P (MC) < 0.006. For sub-regions: AG = Amundsen Gulf, MD = Mackenzie Delta, MS = Mackenzie Shelf/Slope; LS = Lancaster Sound; NW = North Water Polynya; = BB = Baffin Bay; C, E, N, W = central, east, north, west

Regime	Site	t	Df	P (MC)	2008 - 2009	2008	2009
	F Comp						
Hotspots	MD-C	1.750	5	0.0493	56.51	61.29	69.03
	AG-CW	2.302	4	0.0199	39.89	62.98	60.85
	LS-W	1.791	4	0.0573	66.48	77.98	71.62
	LS-E	1.224	4	0.2451	66.86	67.41	71.21
	NW-C	2.691	4	0.0136	52.95	70.55	76.47
	NW-E	1.649	4	0.0774	67.30	75.61	72.13
Coldspots	MS-C	2.223	5	0.0143	49.52	66.88	63.87
	AG-CC	1.167	6	0.2695	55.10	59.67	53.39
	BB-N	1.863	4	0.0549	66.74	72.50	78.15
	T Comp						
Hotspots	MD-C	1.579	5	0.0661	42.32	53.58	49.82
	AG-CW	2.098	4	0.0261	24.70	46.64	50.45
	LS-W	1.532	4	0.0988	47.29	58.87	53.80
	LS-E	1.602	4	0.0744	50.32	59.78	59.50
	NW-C	2.250	4	0.0230	34.64	61.77	53.98
	NW-E	1.316	4	0.1734	52.83	56.22	59.31
Coldspots	MS-C	1.732	5	0.0389	35.99	46.58	52.79
	AG-CC	1.119	6	0.3012	45.23	47.42	45.95
	BB-N	1.796	4	0.0498	54.34	64.33	66.64

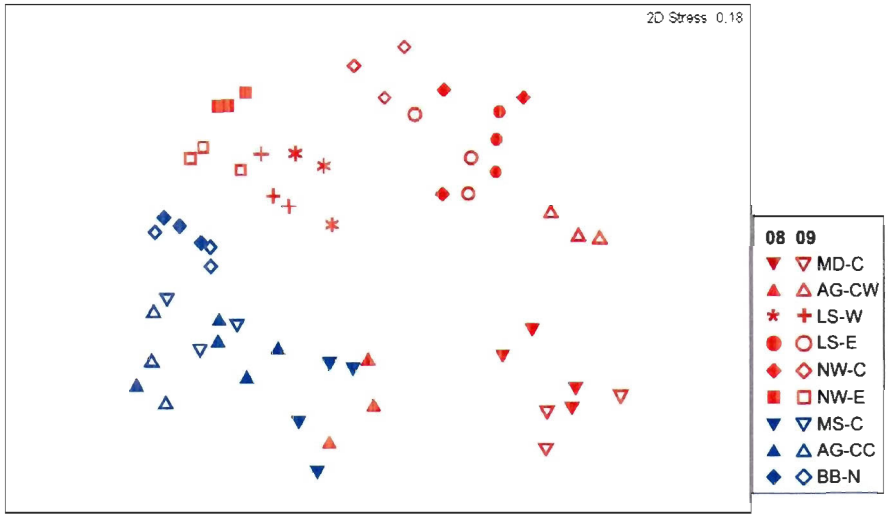

Fig 4.5: Temporal and spatial patterns of taxonomic community composition at each sampling event across the Canadian Arctic in 2008 and 2009. The plot shows the relative similarity of samples in a multidimensional space determined as Bray-Curtis similarity based on 4th-root transformed abundance of taxa. Red = hotspots, blue = coldspots; full symbols = 2008, open symbols = 2009; AG = Amundsen Gulf, MD = Mackenzie Delta, MS = Mackenzie Shelf/Slope; LS = Lancaster Sound; NW = North Water Polynya; = BB = Baffin Bay; C, E, N, W = central, east, north, west.

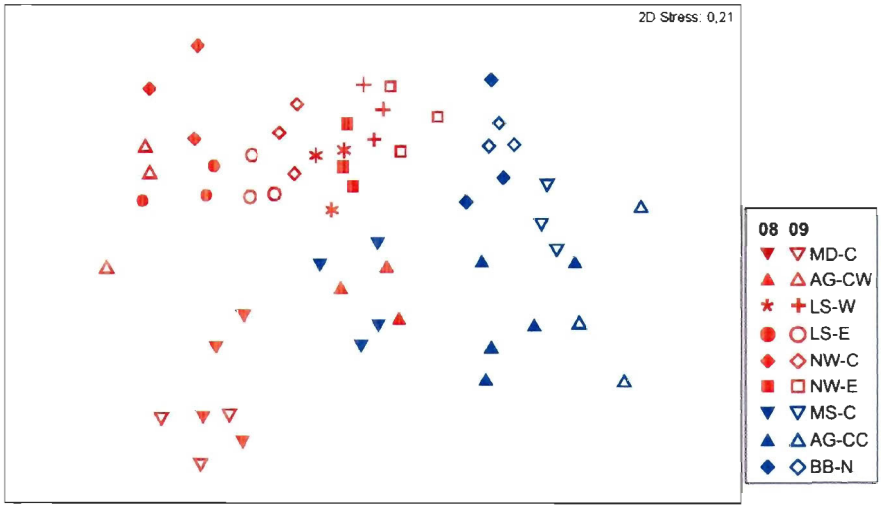

Fig 4.6: Temporal and spatial patterns of functional community composition at each sampling event across the Canadian Arctic in 2008 and 2009. The plot shows the relative similarity of samples in a multidimensional space determined as Bray-Curtis similarity based on 4th-root transformed abundance of functional groups. Red = hotspots, blue = coldspots; full symbols = 2008, open symbols = 2009; AG = Amundsen Gulf, MD = Mackenzie Delta, MS = Mackenzie Shelf/Slope; LS = Lancaster Sound; NW = North Water Polynya; = BB = Baffin Bay; C, E, N, W = central, east, north, west

Influence of biotic and environmental factors on the variability in fluxes

The best distance-based linear model (DistLM), explaining 42 % of the overall variation in benthic boundary fluxes, is composed of five parameters (Fig. 4.7, Table 4.7). Sediment surface Chl *a* concentration contributes most to the explained variation (23.5 %), followed by S_{Tax} (9.5 %), N (5.9 %), water depth (4.3 %) and abundance of *Lumbrineris tetraura* (3.9 %). Measures of functional diversity were not retained in the model. Variation of the first axis mainly separates coldspots from hotspots and pairs of the two years of each site. The most important parameters contributing to the first axis of the dbRDA plot explaining 63 % of fitted flux variation are sediment surface Chl *a* concentration and water depth (Fig. 4.7, Table 4.7). Benthic community parameters were most strongly correlated with the second dbRDA axis explaining 27.9 % of fitted flux variation.

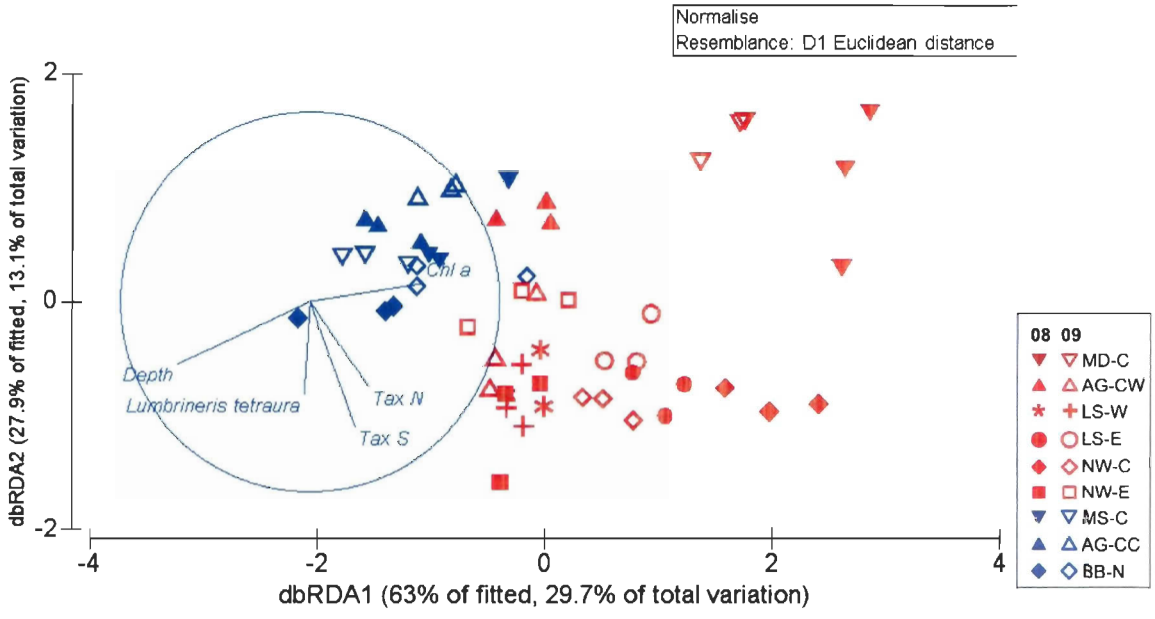

Fig 4.7: Distance-based Redundancy Analysis (dbRDA) plot of the distLM model based on the five parameters fitted to the variation in benthic boundary fluxes (Table 4.7). Vectors indicate direction of the parameter effect in the ordination plot. Chl *a* = Ln of sediment Chl *a* concentration; N = abundance, Tax S = taxonomic richness. Red = hotspots, blue = coldspots; full symbols = 2008, open symbols = 2009; AG = Amundsen Gulf, MD = Mackenzie Delta, MS = Mackenzie Shelf/Slope; LS = Lancaster Sound; NW = North Water Polynya; = BB = Baffin Bay; C, E, N, W = central, east, north, west

Table 4.7: Distance-based linear model (DistLM) of benthic boundary fluxes against environmental and diversity drivers determined in the Canadian Arctic in 2008 and 2009. Proportion of variance in benthic boundary fluxes is explained by environmental variables in stepwise sequential tests following AICc selection criterion. Chl *a* = sediment Chl *a* concentration, S_{Tax} = taxonomic richness, N = individual abundance, Depth = water depth, *L.* = *Lumbrineris*. 'Prop.' is the proportion of variance explained by each single variable, 'Cumul.' is the cumulative proportion of variance explained by multiple variables.

Sequential tests for stepwise model (Adj. R^2 = 42%)

Variable	Adj. R^2[%]	SS(trace)	Pseudo-F	P	Prop.	Cumul.	res.df
Chl *a*	75.693	62.191	15.946	0.0001	0.235	0.235	52
S_{Tax}	70.782	25.168	7.226	0.0001	0.095	0.330	51
N	68.158	15.591	4.811	0.0021	0.059	0.388	50
Depth	66.673	11.344	3.688	0.0069	0.043	0.431	49
L. tetraura	65.34	10.423	3.566	0.0149	0.039	0.471	48

Percentage of multivariate flux variation explained by individual axes

	% explained variation out of fitted model		% explained variation out of total variation	
Axis	Individual	Cumulative	Individual	Cumulative
1	63.01	63.01	29.65	29.65
2	27.87	90.88	13.12	42.77
3	5.92	96.8	2.79	45.56
4	3.19	100	1.5	47.06

Relationships between dbRDA coordinate axes and orthonormal X variables (multiple partial correlations)

Variable	dbRDA1	dbRDA2	dbRDA3	dbRDA4
Chl *a*	0.591	0.092	0.201	0.359
S_{Tax}	0.239	-0.662	0.636	0.025
N	0.314	-0.452	-0.707	0.392
Depth	-0.702	-0.328	0.079	0.516
L. tetraura	-0.031	-0.492	-0.221	-0.671

Discussion

In the Arctic, benthic time-series data are extremely scarce and long-term prediction of the ecosystem function is often based on one-site one-year measures. Here, we focus on

the different patterns of (non-directional) temporal and spatial variability in benthic remineralisation function, functional and taxonomic diversity and resource availability, which we consider important terms of error for long-term predictions. We discuss the role of variability in hotspot *vs* coldspot regimes and finally, we discuss the limitations of a statistical model integrating environmental and macrofaunal parameters to explain directional temporal and spatial variation in benthic remineralisation function in the Arctic.

Hypothesis 1: Benthic remineralisation function is significantly different among years at hotspots but not at coldspots

Simultaneous consideration of five benthic boundary fluxes showed that the magnitude of interannual variability differed between hotspots and coldspots. At hotspot sites the between-years differences were generally more pronounced than at coldspot sites, but the results are less consistent than we assumed. The composition of fluxes at different sites is heterogeneous due to complex interactions with environmental (Farias et al., 2004; Link et al., in press, chapitre 2) and faunal (Michaud et al., 2006; Davenport et al., 2012) parameters. Change in benthic boundary fluxes from one year to another can be positive or negative in its direction, depending on the flux and on the site. This means that a given site x in 2008 can be different from the same site x in 2009, but similar to another site y in 2009 (e.g. LS-W and NW-C, Figs. 4.2, 4.3), although both are hotspots. When remineralisation function as a whole is considered, it is therefore not surprising that the relative change from 2008 to 2009 across all hotspots or all coldspots is not significant, although differences between years are found for four of six hotspots. In fact, the interannual differences at the remaining two hotspots might not be detectable due to the strong within-site variation, but they show the tendency of a shift. The coldspot site BB-N was not only different in 2008 than in 2009, but also differed from other coldspot fluxes. High nitrite uptake of about 30 μmol m^{-2} d^{-1} may be the underlying mechanism. In this study, such high nitrite uptake has only been found at hotspots with other high fluxes (NW-E and LS-E) and typically indicates bacteria-mediated anaerobic degradation of nitrogen derivates such as ammonium

oxidation (anammox). Anammox is considered a common process in deep Arctic cold-water environments, and the nitrite uptake rates measured in 2008 might be a lag response to the degradation of intensive organic matter pulses fuelling abundance and degradation by anammox bacteria (Rysgaard et al., 2004). Site-dependent changes in nutrient fluxes were also found in a shallow-water environment by Thouzeau et al. (2007), who interpreted interannual differences of biogeochemical fluxes as being mostly effected by differences in environmental parameters and organic matter deposition, including indirect effects of macrofauna and macroalgae, depending on the sites. Similar factors could have affected the changes at our hotspot sites.

One of the rare time-series studies including the measurement of total sediment oxygen fluxes in deeper water was conducted in the abyssal north Pacific for eight years (Smith at al., 2001). Although the export of organic matter varied between years, oxygen consumption remained fairly stable. Smith et al. (2001) interpreted this discrepancy in the rather oligotrophic environment they investigated as a capacity of the benthic fauna to endure food deficiency over a limited time period – until a new food pulse arrives. Such an explanation would also fit to oxygen flux patterns of coldspots in our study. Lepore et al. (2007) compared sediment oxygen fluxes (expressed as benthic carbon respiration) among years in the Chukchi Sea in 2002 and 2004. Summed over several sites, they found that benthic carbon respiration did not change much, neither on the shelf nor on the slope, among years, despite great changes in vertical carbon export. One possible explanation for this finding is a time lag in the response of the sediment communities. However, among-site patchiness in benthic carbon respiration was high and may have masked temporal variations at particular sites – as it was the case across hotspots and coldspots in our study. This stresses the importance to separate spatial from temporal variability if we want to understand dynamics of ecosystem functions. A few sites of our study have been sampled prior to 2008. In 2004, Renaud et al. (2007b) reported less than half the oxygen demand (5.65 mmol m^{-2} d^{-1}) of our values at hotspot site MD-C but similar values at hotspot site AG-CW (2.12 mmol m^{-2} d^{-1}). At hotspot site NW-C, the oxygen fluxes we measured in 2008 were twice as high as those measured in 1998 (4.3 mmol m^{-2} d^{-1}, Grant et al., 2002),

but they were largely the same in 2009. Longer time-series measurements are necessary to draw a firm conclusion, but these results may indicate that a progressive change is already happening in the Mackenzie Delta region whereas there is yet a stochastic variability in the NOW region.

We found that differences among sites can be in the same order of magnitude as variations among years (Fig. 4.3). However, the significant difference in remineralisation function between hotspots and coldspots basically confirm our *apriori* categorisation of sites. Although we cannot separate a location from dispersion effect (Anderson et al., 2008) in the data, our results clearly showed that benthic remineralisation function is more variable among years at hotspot sites than at coldspot sites. This means that quantifying progressive directional changes in ecosystem functions at hotspot sites needs long-term series data (Glover et al., 2010), whereas coldspot sites might rather qualify to detect changes through less regular sampling.

Hypothesis 2: Food availability is significantly different among years at hotspots but not at coldspots

Our results showed that the magnitude of interannual variations in food supply to the benthos, as approximated by sediment pigment concentrations, differed between hotspots and coldspots and depends on the considered site. Also, hotspots were different from coldspots. Only one of six hotspot sites but two of three coldspot sites changed significantly over the years. Here, we analysed concentration of rather labile Chl *a* and stable, more degraded phaeopigments in the sediments simultaneously. Phaeopigments can accumulate with degradation of matter and are therefore not necessarily an indicator of recent organic matter input, which we want to detect when looking at annual variability. But since Chl *a* is often rapidly degraded to phaeopigments (Sun et al., 2007), the latter allow the detection of food input even if it had been of lower quality or earlier in the year. Another indicator of food at the seafloor is the ratio of Chl *a* over phaeopigment concentration (e.g. Morata et al., 2008). But as a quality ratio, this measure does not allow to compare the quantity of

pigments at different sites. Since the quality of food is often related to the activity of benthic communities (Sun et al., 2007; Link et al., 2011), we could consider to only use sediment Chl *a* concentration, which should be representative of fresh matter input having occurred in the same season. However, statistical analyses using only sediment Chl *a* did not yield very different results, and only hotspot MS-C differed significantly between years (data not shown). How else can we explain the unexpectedly rare interannual changes at hotspots and more common changes at coldspots? One important issue that could make changes statistically less detectable is the small-scale spatial (within-site) variation in our sediment pigment data (Anderson et al., 2008). Furthermore, dispersion was greater among hotspot sites than among coldspot sites, impeding the detection of changes in the plot. In fact, the results from the SIMPER analysis clearly showed that hotspots were more different from one year to another than coldspots, but also that the difference between years for coldspots was large compared to the variability among coldspots of the same year.

Interannual changes of sediment pigments were found at several depths in the Fram Strait at the HAUSGARTEN site in Norway (Soltwedel et al., 2005), which could be related to a decrease in settling phytodetrital matter. In our study area, interannual variability of vertical flux patterns is only known for part of the study period and study area. Sallon et al. (2011) found two-day vertical fluxes at hotspots MS-C and AG-CW in 2008 that were similar to those reported in 2004 (Juul-Pedersen et al., 2010). Both were higher than those determined in the 1980ies (O'Brien et al., 2006). Recent results from 2009 showed, however, that vertical fluxes at theses sites were lower than in 2008 (Forest et al., 2012.; Link et al., in press, chapitre 2). Due to the generally tight pelagic-benthic coupling in the Arctic, such interannual variability in vertical fluxes in the southeastern Beaufort Sea (see also Forest et al., 2010 for a more regional approach) could lead to interannual sediment pigment changes, even at coldspots. In the NOW, at the hotspots NW-C and NW-E, Hargrave et al. (2002) showed an about two-fold increase of vertical flux from 1998 to 1999. In the LS-W region, strong interannual variability of processes determining pelagic-benthic coupling, including the release of ice algae, have been observed between 1984 and 1992 (Michel et al., 2006). However, in that period the change

seemed stochastic and we may have sampled in two years of similar vertical export. Although these regions show interannual variability, we do not know how or whether vertical fluxes changed between 2008 and 2009, and it is therefore difficult to explain the lack of signal for sediment pigments using vertical flux patterns. To our knowledge, no data on vertical fluxes in the area of LS-E or BB-N has been published, thus that we can only infer variability from primary production and phytoplankton Chl *a* biomass patterns. Significant interannual differences between 2005 and 2007 (confounded with season late summer, early fall and fall) in primary production have not been found for the Beaufort Sea, Archipelago (including Lancaster Sound) or NOW (Ardyna et al., 2011). However, phytoplanktion Chl *a* biomass at individually resampled sites AG-CW (408), AG-CC (405), NW-C (108) and NW-E (115) seemed different in 2005 than in 2006 and 2007. But at water depths of more than 200 m, several processes influence the actual export of primary production to the seafloor. Temporal and spatial variability in these pelagic processes may nullify or even invert an increase in primary production to a decrease in vertical export, as has been reported at some sites in the southeastern Beaufort Sea in 2008 (Sallon et al., 2011; Forest et al., 2011). Such discrepancy is particularly evident for site AG-CC, which Ardyna et al. (2011) identified as a hotspot of primary production, but which is consistently a coldspot in benthic parameters. Lateral advection has been proposed as mechanism underlying discrepancies between surface primary production and benthic activity (Lepore et al., 2007). However, currents in the central Amundsen Gulf region are generally weak, thus that pelagic degradation is probably more important (Forest et al., 2010, 2011). Extrapolating temporal and spatial changes in benthic food supply from primary production patterns should be treated with extreme caution.

Benthic degradation of organic matter could theoretically also be the reason why coldspots with consistently lower sediment pigment concentration demonstrate more changes than hotspots: Assuming that hotspots generally host higher abundance of organisms due to generally higher food supply (e.g. Rex et al., 2006), such higher density could consume a peak of arriving food more rapidly than a site with lower abundance. Rapid consumption of organic material has been demonstrated for seafloor communities of

different depths (Witte et al., 2003) and Arctic locations (Link et al., 2011; Sun et al., 2007). If sediment food supply is measured months after the input peak, the measured sediment pigments could represent the 'leftovers of the feast', which should vary less when abundance is high. Our data does not support the hypothesis that food supply varies more among years at hotspots than at coldspots. The results indicate that when explaining changes in benthic function, the interaction of community composition on measured food supply (i.e. the remaining stock) could influence the results.

Hypothesis 3: Taxonomic community composition is not significantly different among years

Macrobenthic communities at hotspots or coldspots in the Canadian Arctic did not change significantly in taxonomic composition from 2008 to 2009. Instead, the community composition is generally different at hotspots than that at coldspots, and sites are distinct from each other. The total number of 331 macrobenthic taxa found in our samples may seem low compared to the overall number of 992 taxa reported from the entire Canadian Arctic (Archambault et al., 2010). Piepenburg et al. (2011) performed a rarefaction analysis based on molluscs, arthropods, echinoderms and annelids for different regions in the Arctic. They showed that 19 sampling events would yield an average of 274 observed taxa in the Amundsen Gulf region and 205 on the Beaufort Shelf. Moreover, based on less stations, totals of 86 and 204 taxa have been reported for Lancaster Sound and northern Baffin Bay, respectively (Piepenburg et al., 2011). Considering species overlap between the different regions and a total of 18 sampling events, we can assume to have taken and analysed a typical number of species for the sampling size. The number of taxa we found at sites in the NOW region was also lower than reported by Lalande (2003). But due to the different sampling approaches applied (here: 3 incubation cores of 80 cm^2 each *vs* large corers covering areas of usually 1250 cm^2), our results are not directly comparable, and the numbers most likely only represent differences in total sampled surface. Two data distribution patterns in the MDS plot (Fig.5) are interesting to note: First, with the exception of site AG-CW 2008, hotspot sites are well separated from coldspot sites. This

observation confirms the notion that species composition is largely dependent on regimes of food supply (Smith et al., 2008), since primary production regimes were part of our hotspot definition. Second, sites are clustered according to their depth within the hotspot or coldspot groups (which is much less the case for benthic fluxes) (Fig. 4.5). This indicates depth zonation of benthic infauna communities on a shelf gradient, which has previously been reported (Conlan et al., 2008; Hoste et al., 2007), but could not be identified by Cusson et al. (2007) in other regions of the Canadian Arctic. These results of within-regime gradients stress the importance that environmental factors other than depth create communities of different diversity and composition.

In contrast to spatio-temporal patterns in benthic boundary fluxes and sediment pigments, the significant interaction between the factors year and site in our data results only from statistically different pairs of different sites across years. Similar variability of communities across sites in 2008 and 2009 is also confirmed through the SIMPER analysis. Polar environments host species with longer life spans, and community turnover rates should therefore be slower. In an arctic Fjord, Kedra et al. (2010) reported a decadal shift in communities in two of the fjord regions influenced by an intrusion of warm water, but no changes in a third region with more stable hydrographic conditions. This supports the notion that community changes are rather long-term reactions to environmental forcing. Similarly, long-term time series of macrobenthic infauna in the northern Bering Sea show progressive change in community composition since 2000 on a decadal scale, although the change is not yet statistically detectable (Grebmeier, 2012). At sites in Frobisher Bay (Canadian Arctic), however, Cusson et al. (2007) detected monthly variability in community composition. Considering that those communities became similar over time again, the effect of lacking replicate data information could have reduced both within-month and within-site variability and thus produced an artificial signal. The overall low within-site variability of Frobisher Bay sites compared to other sites in the Canadian Arctic supports this explanation. Interannual variations in meiofaunal abundance were found during time-series measurements at the HAUSGARTEN from 2000-2004 (Hoste et al., 2007). However, these changes were less clear when community composition was

considered. Overall, the results support our hypothesis and spatial variability in community composition seems more pronounced than interannual variations. However, without separating the temporal from the spatial component of variability, we will miss out detecting long-term shifts in community composition, such as that reported by Grebmeier (2012) in the northern Bering Sea.

Hypothesis 4: Functional community composition is not significantly different among years

The number of 72 functional groups reported in our study may seem very high, but if functional groups are to be related to ecosystem functions, it is crucial to include as many different trait categories as known to influence those functions (Petchey and Gaston, 2006). We therefore think that such fine-scale categorisation is adequate. Functional richness (number of functional groups) was largely similar to the number of taxa at sites with only few taxa, but was clearly lower at sites with many taxa (Table S4.2). This is a typical phenomenon, since in small-scale studies, the probability to find species redundant in their functions increases with the total number of species encountered (Cumming and Child, 2009). Functional diversity can follow changes in taxonomic diversity – or not (Hooper et al., 2005; Villeger et al., 2012). If functional redundancy is present (as for samples where taxonomic diversity is higher than functional diversity), a reduction in the number of species will not necessarily decrease the number of functional groups. This implies less variability, and the absence of changes in functional composition over the years matches well with temporal patterns in taxonomic composition.

When comparing results of variation in functional composition and taxonomic composition, we again find a well-defined separation of hotspot and coldspot sites. However, sites are generally more similar to each other when functional diversity is analysed. Using functional diversity in comparative studies has received increasing attention over the last decades (Naeem et al., 2012). An important advantage of this approach is its lower susceptibility to misclassifications, and Cochrane et al. (2012) have recently demonstrated its utility to describe ecologically distinct regions in the Barents Sea.

Although the general power to identify spatial and temporal differences in community composition is reduced when the functional (opposed to taxonomic) approach is used, it is sufficient to describe the ecological role of different communities.

Hypothesis 5: Food supply explains temporal variation and macrofaunal community parameters explain spatial variation in benthic remineralisation function

The results of this study confirm our hypothesis that the temporal variability of benthic remineralisation function is most affected by sediment pigments while its spatial variation is largely determined by diversity patterns. However, water depth was an additional important factor explaining spatial patterns, both among sites and between hotspots and coldspots. We demonstrated how depth played a role in explaining the resemblance patterns in taxonomic community composition (see section H3). Moreover, water depth has been used as a rough estimate for food supply to the benthos (Graf, 1992), as also indicated by its similar relationship to the variation axes as that of sediment Chl *a* concentrations in our data. The importance of an easy-to-determine and steady-state variable for ecosystem functions can have stabilizing effects in predicting models, but also calls for caution considering its low explicative power and when ecosystems of different depths and regimes are compared (Glover et al., 2010). In our data, sediment Chl *a* concentrations are strongly related to the variation axis across which hot- and coldspots are separated, and along which temporal variability of sites is spread, despite the lack of temporal variability in the variable itself. The retention of Chl *a* but not phaeopigments in our model underpins the notion that fresh food supply rather than general food supply is most important in determining benthic remineralisation function (Sun et al., 2007; Link et al., 2011; Link et al., in press, chapitre 2).

About 20 % of the variation in benthic function is explained by different measures of diversity (richness of taxa, individual abundance, and the abundance of *L. tetraura*). These three variables mostly explain differences between hotspots and coldspots and the eastern and western Canadian Arctic, but also temporal variation at hotspots AG-CW and NW-E.

The better explicative power of taxonomic *vs* functional group richness may be due to several mechanisms. Resource availability, measured as Chl *a* in our study, may affect the diversity-ecosystem function relationship. At large spatial scales across the marine Arctic, the number of benthic species generally increases with primary production, if the effect of salinity is removed from the model (Witman et al., 2008). If functional group richness is more related to sediment Chl *a* concentration, then taxonomic richness is chosen as a more complementary variable to the already used Chl *a* in the model. Moreover, interactions between functional and species richness in their effect on functions have been found, making species richness more important, if functional richness is low (Wahl et al., 2011). Another cause for taxonomic richness being more important is the use of multiple processes defining our function: Using multiple processes decreases the chance that several species are redundant in effecting the functions (Gamfeldt et al., 2008).

Our statistical approach of a predictive linear model does not allow testing the combined effect of food supply and community composition on multiple benthic fluxes. But total abundance and the abundance of a gallery-burrowing polychaet species as significant predictors for multiple benthic functions stress the importance of community composition additionally to mere species numbers. In fact, the density of fauna (Braeckman et al., 2010), identity or functional traits of species (Michaud et al., 2006; Piot, 2012) and the number of burrows at the seafloor (Davenport et al., 2012) have been related to benthic boundary fluxes before.

More than half of the variation in benthic boundary fluxes in our data could not be explained by our best model. As already mentioned above, more exact measures of community composition or trait composition could explain more variation. Two other important benthic community components are also lacking in our study: meiobenthic and bacterial abundance. The role of meiobenthos for biogeochemical cycles is less studied, but there is increasing evidence that its density is related to benthic remineralisation function (Veit-Köhler et al., 2011; Nascimento et al., 2012; Piot, 2012). The role of bacteria on the other hand is well known to be important for organic matter degradation processes

(Jørgensen, 2006). Different types of bacteria can influence the particular process of degradation (e.g. anammox), can react rapidly to matter input and interact with macrofaunal matter degradation processes (Boetius and Damm, 1998; Rysgaard et al., 2004; Hunter et al., 2012). Although evidence is increasing that macrofauna drives the variability in bacteria-mediated degradation (Michaud et al., 2009; Hunter et al., 2012), future studies should integrate meiofaunal and microbenthic organisms to gain a better understanding of mechanisms regulating temporal and spatial variability of benthic remineralisation function.

Benthic ecosystem function in the Canadian Arctic increases with fresh food supply, species-rich and functional diverse communities and decreasing depth. With climate change, the quantity and – even more importantly - the quality of food supply to polar benthos is altering (Forest et al., 2011; Tremblay et al., 2011; Wassmann et al., 2011). While we currently still know only little about how benthic communities will react to these changes (Grebmeier, 2012), we could show here that diversity changes will have an impact on the quality of benthic ecosystem functioning, depending on resource availability.

Conclusion

Great efforts are underway to estimate the impact of climate change on polar ecosystems. Due to the very limited number of real benthic time-series measurements in the Arctic, ecosystem models often rely on data obtained from different sites at different times of the year. One important question under these circumstances is: Are known benthic diversity hotspots in the Canadian Arctic also hotspots in ecosystem function? We conclude from our findings: Yes, with regard to a general spatial comparison, but no, with regard to long-term predictions, which may increase variability of resource availability due to climate-related ecological change. In our study, we have demonstrated that the influence of diversity on multiple benthic ecosystem functions is complementary or dependent on the availability of resources. The mechanisms controlling temporal variability of factors explaining benthic ecosystem function vary even on a within-region spatial scale. We have

also shown that the similarity in taxonomic and functional diversity patterns indicate little insurance against the climate induced species loss in the Canadian Arctic. Even models that include several variables (steady-state ones but also those varying on short and long time scales) explained only half of the variability in multiple benthic ecosystem function in the Canadian Arctic. Defining the role of the functional identity of particular organisms in benthic biogeochemical cycles should help to better predict benthic remineralisation processes. Our findings also strongly suggest that for reliable predictions of how ecosystem functioning in Arctic shelf habitats will change in the future and how close we are to tipping points, it is necessary to establish time-series sites at hotspots and coldspots where multiple function measures are monitored, in order to distinguish natural oscillations from directional change.

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Table S4.1: Taxa list. The table presents all taxa identified during this study and the accorded functional traits. For details on functianal trait categories and levels, see Table 4.2.

Class	**Species/taxon**	Feeding	Size	Motility	Bioturbation
Oligochaeta	*Oligochaeta sp.*	S	L	M	T
Polychaeta	*Ophryotrocha sp.*	O	S	M	S
Polychaeta	*Schistomeringos caeca*	C	S	M	B
Polychaeta	*Schistomeringos rudolphii*	C	M	M	B
Polychaeta	*Lumbrineris scopa*	OC	L	M	G
Polychaeta	*Lumbrineris sp.*	OC	M	M	G
Polychaeta	*Lumbrineris sp. 1*	OC	M	M	G
Polychaeta	*Lumbrineris sp. 2*	OC	M	M	G
Polychaeta	*Lumbrineris sp. 3 cf. fauchaldi*	OC	L	M	G
Polychaeta	*Lumbrineris sp. 4 cf. fragilis*	OC	L	M	G
Polychaeta	*Lumbrineris tetraura/impatiens*	C	L	M	G
Polychaeta	*Nothria conchylega*	O	L	H	S
Polychaeta	*Paradiopatra quadricuspis*	OC	L	H	S
Polychaeta	*Chrysopetalidae sp.*	C	M	M	S
Polychaeta	*Hesionidae sp.*	O	M	M	B
Polychaeta	*Nereimyra sp.*	C	M	M	B
Polychaeta	*Aglaophamus malmgreni*	C	M	M	G
Polychaeta	*Bipalponephtys neotena*	C	M	M	G
Polychaeta	*Micronephtys minuta*	C	S	M	G
Polychaeta	*Nephtyidae sp. 2*	C	M	M	G
Polychaeta	*Nephtyidae sp. 1 cf. Nephtys*	C	M	M	G
Polychaeta	*Nephtys ciliata*	C	L	M	G
Polychaeta	*Pholoe longa*	C	M	M	B
Polychaeta	*Pholoe sp.*	C	S	M	B
Polychaeta	*Eteone flava/longa*	CO	L	M	B
Polychaeta	*Eteone sp.*	CO	L	M	B
Polychaeta	*Phyllodoce sp.*	CO	L	M	B
Polychaeta	*Bylgides sarsi*	C	L	M	S
Polychaeta	*Eucranta sp.*	C	L	M	S
Polychaeta	*Eucranta villosa*	C	L	M	S
Polychaeta	*Gattyana cirrosa*	C	L	M	S
Polychaeta	*Polynoidae*	C	L	M	B
Polychaeta	*Polynoidae sp. 1*	C	L	M	B
Polychaeta	*Clavodorum sp.*	D	S	M	S
Polychaeta	*Sphaerodoropsis sp. 2*	D	S	M	S
Polychaeta	*Sphaerodoropsis sp. 1 cf. furca*	D	S	M	S
Polychaeta	*Sphaerodorum gracilis*	D	S	M	S
Polychaeta	*Anguillosyllis pupa*	D	S	M	S
Polychaeta	*Anguillosyllis sp.*	D	M	M	S
Polychaeta	*Erinaceusyllis sp.*	D	S	M	S
Polychaeta	*Exogone naidina*	D	S	M	S
Polychaeta	*Exogoninae sp.*	D	S	M	S
Polychaeta	*Prosphaerosyllis sp. nov.*	D	S	M	S
Polychaeta	*Streptosyllis sp. nov. 1*	CO	S	M	S
Polychaeta	*Streptosyllis sp. nov. 2*	CO	S	M	S
Polychaeta	*Syllis sp.*	C	M	M	S

Table S4.1 continued

Class	Species/taxon	Feeding	Size	Motility	Bioturbation
Polychaeta	*Galathowenia*	D	M	H	T
Polychaeta	*Galathowenia oculata*	D	M	H	T
Polychaeta	*Myriochele heeri*	D	M	H	T
Polychaeta	*Myriochele olgae*	D	M	H	T
Polychaeta	*Myrioglobula malmgreni*	DF	L	H	T
Polychaeta	*Owenia borealis*	DF	L	H	T
Polychaeta	*Owenia polaris*	DF	L	H	T
Polychaeta	*Owenia sp.*	DF	L	H	T
Polychaeta	*Chone sp.*	F	L	S	T
Polychaeta	*Euchone analis*	F	L	S	T
Polychaeta	*Euchone incolor*	F	L	S	T
Polychaeta	*Jasmineira schaudinni*	F	L	S	T
Polychaeta	*Jasmineira sp.*	F	L	S	T
Polychaeta	*Oriopsis sp.*	F	L	S	T
Polychaeta	*Sabellidae sp.*	F	L	S	T
Polychaeta	*Spirorbis sp.*	F	M	S	S
Polychaeta	*Capitella capitata*	S	L	H	G
Polychaeta	*Capitellidae sp.*	S	L	H	G
Polychaeta	*Hetero- or Mediomastus*	S	L	H	G
Polychaeta	*Heteromastus filiformis*	S	L	H	G
Polychaeta	*Heteromastus sp.*	S	L	H	G
Polychaeta	*Notomastus sp.*	S	L	M	B
Polychaeta	*Cossura pygodactyla*	S	M	H	T
Polychaeta	*Cossura sp.*	S	M	M	B
Polychaeta	*Asychis biceps*	S	L	S	T
Polychaeta	*Asychis sp. 1*	S	L	S	T
Polychaeta	*Clymenura polaris*	S	L	S	T
Polychaeta	*Clymenura sp. 1*	S	L	S	T
Polychaeta	*Lumbriclymeninae sp.*	S	L	S	T
Polychaeta	*Maldane arctica*	S	L	S	T
Polychaeta	*Maldane glebifex*	S	L	S	T
Polychaeta	*Maldane sarsi*	S	L	S	T
Polychaeta	*Maldane sp. (arctica + sarsi)*	S	L	S	T
Polychaeta	*Maldanidae sp. 1*	S	L	S	T
Polychaeta	*Maldanidae sp. 2*	S	L	S	T
Polychaeta	*Maldanidae sp. 3*	S	L	S	T
Polychaeta	*Maldanidae sp. 4*	S	L	S	T
Polychaeta	*Maldanidae sp. 5*	S	L	S	T
Polychaeta	*Maldanidae sp. 6*	S	L	S	T
Polychaeta	*Maldanidae spp.*	S	L	S	T
Polychaeta	*Nicomache cf. lumbricalis*	S	L	S	T
Polychaeta	*Nicomache quadrispinata*	S	L	S	T
Polychaeta	*Nicomachenae/Petaloproctus*	S	L	S	T
Polychaeta	*Petaloproctus tenuis*	S	L	S	T
Polychaeta	*Praxillela affinis*	S	L	S	T
Polychaeta	*Praxillela gracilis*	S	L	S	T
Polychaeta	*Praxillela/axiothella*	S	L	S	T
Polychaeta	*Ophelina cylindricaudata*	S	M	M	G
Polychaeta	*Ophelina sp. 2*	S	M	M	G
Polychaeta	*Ophelina sp. 1 cf. breviata*	S	M	M	G

Table S4.1 continued

Class	Species/taxon	Feeding	Size	Motility	Bioturbation
Polychaeta	*Scoloplos sp. 2*	S	L	M	B
Polychaeta	*Scoloplos sp. 1 cf. acutus ou armiger*	S	L	M	B
Polychaeta	*Aricidea fragilis*	D	M	H	B
Polychaeta	*Aricidea nolani*	D	M	H	G
Polychaeta	*Aricidea quadrilobata*	D	M	H	G
Polychaeta	*Aricidea sp. 1*	D	M	H	G
Polychaeta	*Aricidea sp. 2*	D	M	H	G
Polychaeta	*Aricidea sp. 3 cf. hartmani*	D	M	H	G
Polychaeta	*Aricidea sp. 4*	D	M	H	G
Polychaeta	*Aricidea suecica*	DF	M	H	G
Polychaeta	*Levinsenia (Paraonis) gracilis*	D	M	H	G
Polychaeta	*Paraonidae*	D	M	H	G
Polychaeta	*Scalibregma inflatum*	S	S	M	B
Polychaeta	*Scalibregmatidae sp.*	S	S	M	B
Polychaeta	*Apistobranchus sp. cf. tullbergi*	D	M	H	T
Polychaeta	*Spiochaetopterus sp. cf. typicus*	DF	L	S	T
Polychaeta	*Dipolydora caulleryi*	DF	M	H	T
Polychaeta	*Dipolydora sp.*	DF	M	H	T
Polychaeta	*Laonice sp. cf. cirrata*	DF	M	H	T
Polychaeta	*Polydora/Dipolydora*	DF	M	H	T
Polychaeta	*Prionospio cirrifera*	DF	M	H	T
Polychaeta	*Prionospio sp.*	DF	M	H	T
Polychaeta	*Prionospio steenstrupi*	DF	M	H	T
Polychaeta	*Spio sp.*	DF	M	H	T
Polychaeta	*Spionidae w/o branchia*	D	M	H	T
Polychaeta	*Trochochaeta multisetosa*	D	L	S	T
Polychaeta	*Trochochaeta watsoni*	D	L	S	T
Polychaeta	*Amage gallasii*	DF	M	M	B
Polychaeta	*Amage sp. cf. auricula*	DF	M	H	B
Polychaeta	*Ampharete finmarchica*	D	L	S	T
Polychaeta	*Ampharete sp.*	D	L	S	T
Polychaeta	*Ampharetidae sp. 1*	D	L	S	T
Polychaeta	*Ampharetidae sp. 2 = Amythasides*	D	L	S	T
Polychaeta	*Ampharetidae sp. 3*	D	L	S	T
Polychaeta	*Ampharetidae juv*	D	M	S	T
Polychaeta	*Ampharetinae sp.*	D	L	S	T
Polychaeta	*Ampharetinae sp. 1*	D	L	S	T
Polychaeta	*Ampharetinae sp. 2*	D	L	S	T
Polychaeta	*Ampharetinae sp. 3*	D	L	S	T
Polychaeta	*Ampharetinae sp. 4*	D	L	S	T
Polychaeta	*Amphicteis gunneri*	D	L	S	T
Polychaeta	*Auchenoplax sp.*	D	L	S	T
Polychaeta	*Glyphanostomum pallescens*	D	L	S	T
Polychaeta	*Pterolysippe vanelli*	D	M	H	B
Polychaeta	*Sabellides borealis*	DF	L	S	T
Polychaeta	*Aphelochaeta sp.*	D	L	H	B
Polychaeta	*Chaetozone sp. 1 cf. setosa*	D	M	M	B
Polychaeta	*Chaetozone sp. 2*	D	M	M	B
Polychaeta	*Chaetozone/Tharyx*	D	M	M	B
Polychaeta	*Cirratulidae*	D	L	H	B

Table S4.1 continued

Class	Species/taxon	Feeding	Size	Motility	Bioturbation
Polychaeta	*Monticellina sp.*	D	M	H	B
Polychaeta	*Tharyx sp.*	D	M	H	B
Polychaeta	*Brada villosa*	D	L	H	S
Polychaeta	*Diplocirrus hirsutus*	D	M	H	S
Polychaeta	*Diplocirrus sp. 1 cf. longisetosus*	D	M	H	S
Polychaeta	*Flabelligeridae*	D	M	H	S
Polychaeta	*Cistenides hyperborea*	S	L	M	B
Polychaeta	*Paramphitrite sp.*	D	L	S	T
Polychaeta	*Pista sp.*	D	L	S	T
Polychaeta	*Polycirrus arcticus*	D	L	H	T
Polychaeta	*Polycirrus sp.*	D	L	H	T
Polychaeta	*Proclea graffi*	D	L	S	T
Polychaeta	*Proclea malmgreni*	D	L	S	T
Polychaeta	*Terebellidae sp. 1*	D	L	S	T
Polychaeta	*Terebellidae sp. 2*	D	L	S	T
Polychaeta	*Terebellinae (Amphitritinae) sp.*	D	L	S	T
Polychaeta	*Thelepodinae*	D	L	S	T
Polychaeta	*Terebellides bigeniculatus*	D	L	S	T
Polychaeta	*Terebellides cf. williamsae*	D	L	S	T
Polychaeta	*Terebellides sp.*	D	L	S	T
Polychaeta	*Terebellides stroemi*	D	L	S	T
Polychaeta	*Terebellomorpha sp. 1*				
Polychaeta	*Terebellomorpha sp. 2*				
Malacostraca	*Byblis gaimardii*	F	L	H	S
Malacostraca	*Haploops oonah*	F	L	H	S
Malacostraca	*Haploops sp.*	F	L	H	S
Malacostraca	*Haploops tubicola*	F	L	H	S
Malacostraca	*Argissa hamatipes*	S	L	M	B
Malacostraca	*Caprella septentrionalis*	D	L	M	S
Malacostraca	*Gammaridae*	D	M	M	B
Malacostraca	*Paraphoxus oculatus*	D	M	M	B
Malacostraca	*Isaiedae sp.*	F	L	H	B
Malacostraca	*Ischyrocerus megacheir*	F	M	M	B
Malacostraca	*Ischyrocerus sp.*	F	M	M	B
Malacostraca	*Lysianassidae sp.*	O	L	M	S
Malacostraca	*Paracentromedon sp.*	O	L	M	S
Malacostraca	*Paronesimus sp.*	O	L	M	S
Malacostraca	*Aceroides latipes*	C	M	M	B
Malacostraca	*Bathymedon sp. cf. Obtusifrons*	C	M	M	B
Malacostraca	*Oediceropsis brevicornis*	C	M	M	B
Malacostraca	*Oedicerotidae*	C	M	M	B
Malacostraca	*Paroediceros sp.*	C	M	M	B
Malacostraca	*Halice sp.*	S	M	H	B
Malacostraca	*Pardaliscidae sp.*	S	M	H	B
Malacostraca	*Pontoporeia femorata*	D	M	M	B
Malacostraca	*Diastylidae sp. 1*	DF	M	M	S
Malacostraca	*Diastylidae sp. 2*	DF	M	M	S
Malacostraca	*Diastylis lucifera*	DF	M	M	S
Malacostraca	*Diastylis rathkei*	DF	M	M	S
Malacostraca	*Diastylis sp.*	DF	M	M	S

Table S4.1 continued

Class	Species/taxon	Feeding	Size	Motility	Bioturbation
Malacostraca	*Ektonodiastylis nimia/Brachydiastylis*	DF	M	M	S
Malacostraca	*Eudorella emarginata*	DF	M	M	S
Malacostraca	*Eudorella sp.*	DF	M	M	S
Malacostraca	*Eudorellopsis integra*	DF	M	M	S
Malacostraca	*Leucon acutirostris*	DF	M	M	S
Malacostraca	*Leucon fulvus*	DF	M	M	S
Malacostraca	*Leucon nasicus*	DF	M	M	S
Malacostraca	*Leucon sp.*	DF	M	M	S
Malacostraca	*Leuconidae sp. 1*	DF	M	M	S
Malacostraca	*other 1*	DF	M	M	S
Malacostraca	*other 2*	DF	M	M	S
Malacostraca	*Saduria sabini*	C	L	M	S
Malacostraca	*Desmosoma lineare*	S	S	M	B
Malacostraca	*Eugerda tenuimana*	S	S	M	B
Malacostraca	*Caecognathia stygia*	P	M	H	S
Malacostraca	*Gnathia sp.*	P	M	H	S
Malacostraca	*Synidotea bicuspida*	D	L	M	S
Malacostraca	*Ilyarachna hirticeps*	C	M	M	S
Malacostraca	*Pleurogonium spinosissimum*	S	M	M	B
Malacostraca	*Leptognathia sp.*	D	M	H	S
Malacostraca	*Akanthophoreus gracilis*	D	S	H	S
Malacostraca	*Akanthophoreus sp. cf. disa*	D	S	H	S
Malacostraca	*Pseudotanais affinis*	D	M	H	S
Malacostraca	*Pseudotanais forcipatus*	D	M	H	S
Malacostraca	*Pseudotanais sp.*	D	M	H	S
Malacostraca	*Pseudosphyrapus serratus*	C	M	M	B
Malacostraca	*Typhlotanais sp.*	D	S	H	S
Malacostraca	*Tanaidae*	D	S	H	S
Ostracoda	*Cypridininae*	CO	S	M	S
Ostracoda	*Philomedes sp. 1*	D	S	M	S
Ostracoda	*Philomedes sp. 2 cf. brenda*	D	S	M	S
Ostracoda	*Scleroconcha sp.*	D	S	M	S
Ostracoda	*Myodocopida*	D	S	M	S
Ostracoda	*Hemicytheridea sp.*	CO	S	M	S
Ostracoda	*Sarsicytheridea sp.*	CO	S	M	S
Ostracoda	*Trachyleberididea sp.*	CO	S	M	S
Ostracoda	*Acanthocythereis sp. cf. dunelmensis*	CO	S	M	S
Ostracoda	*Podocopida (Ostracoda B)*	CO	S	M	S
Pycnogonida	*Nymphon sp. 1 cf. hirtum*	C	L	M	S
Pycnogonida	*Nymphon sp. 2 cf hirtipes*	C	L	M	S
Pycnogonida	*Nymphon sp. 3*	C	L	M	S
Bryozoa	*Bryozoa*	F	L	S	S
Gymnolemata	*Notoplites sp.*	F	M	S	S
Gymnolemata	*Eucratea loricata*	F	L	S	S
Gymnolemata	*Romancheinidae sp.*	F	L	S	S
Gymnolemata	*Alcyonidium sp.*	F	M	S	S
Gymnolemata	*Alcyonidium sp. 2*	F	M	S	S
Priapulida	*Priapulida*	S	L	H	B
Priapulida	*Priapulopsis bicaudatus*	S	L	H	B

Table S4.1 continued

Class	Species/taxon	Feeding	Size	Motility	Bioturbation
Ascidiacea	*Phlebobranchia sp.*	F	L	S	S
Ascidiacea	*Polycarpa*	F	M	S	S
Ascidiacea	*Ascideacea sp. 1*	F	M	S	S
Ascidiacea	*Ascideacea sp. 2*	F	M	S	S
Anthozoa	*Actinostolidae sp.*	FCO	L	S	S
Anthozoa	*Edwardsidae*	C	M	H	B
Anthozoa	*Athenaria sp. cf. halcampa*	C	M	H	B
Anthozoa	*Actinaria sp.*	C	M	H	S
Anthozoa	*Cerianthidae sp.*	C	L	H	B
Anthozoa	*Anthozoa sp. 1*	C	M	H	S
Anthozoa	*Anthozoa sp. 2*	C	M	H	S
Hydrozoa	*Anthoathecata*	FCO	L	S	S
Hydrozoa	*Obelia sp.*	FCO	L	S	S
Hydrozoa	*Sertularia sp.*	FCO	L	S	S
Hydrozoa	*Sertulariidae spp.*	FCO	L	S	S
Hydrozoa	*Thuiaria sp.*	FCO	L	S	S
Hydrozoa	*Tiaropsis multicirrata*	FCO	M	M	S
Hydrozoa	*rhizome*	FCO	L	S	S
Asteroidea	*Asteroidea*	C	L	M	S
Asteroidea	*Ctenodiscus crispatus*	DO	L	M	B
Echinodermata	*Echinoderm larvae*	D	L	M	S
Holothuroidea	*Holothuridae sp. 1*	D	M	M	B
Holothuroidea	*Holothuridaesp. 2*	D	M	M	B
Holothuroidea	*Holothuridae sp. 3*	D	M	M	B
Ophiuroidea	*Ophiocten sericeum*	DO	L	M	S
Ophiuroidea	*Ophiuroidea*	DO	L	M	S
Enteropneusta	*Enteropneusta*	D	L	M	B
Bivalvia	*Cuspidaria sp. cf. glacialis*	C	L	H	B
Bivalvia	*Cuspidariidae*	C	M	H	B
Bivalvia	*Bathyarca sp.*	F	M	S	S
Bivalvia	*Astarte sp. 1 cf. elliptica ou esquimati*	F	L	H	B
Bivalvia	*Astarte sp. 2 cf. montagui*	F	L	H	B
Bivalvia	*Limidae*	F	M	S	S
Bivalvia	*Bivalvia sp. 2 (Thyasiridae)*	F	M	H	B
Bivalvia	*Thyasira sp. (east)*	F	M	H	B
Bivalvia	*Thyasira sp. (west)*	F	M	H	B
Bivalvia	*Crenella faba*	F	L	S	S
Bivalvia	*Dacrydium*	F	M	S	S
Bivalvia	*Dacrydium viviparum*	F	M	S	S
Bivalvia	*Musculus glacialis*	F	L	S	S
Bivalvia	*Musculus niger*	F	L	S	S
Bivalvia	*Mytilidae*	F	M	S	S
Bivalvia	*Portlandia sp. cf. frigida*	S	M	H	B
Bivalvia	*Ennucula tenuis*	S	M	M	B
Bivalvia	*Nucula sp.*	S	M	M	B
Bivalvia	*Montacuta sp.*	F	M	S	B
Bivalvia	*Montacutidae sp.*	F	M	S	B
Bivalvia	*Macoma calcarea*	DF	L	H	B
Bivalvia	*Bivalvia decalcifié*	DF	M	H	B

Table S4.1 continued

Class	Species/taxon	Feeding	Size	Motility	Bioturbation
Bivalvia	*Bivalvia sp. 1*	DF	M	H	B
Bivalvia	*Bivalvia sp. 3*	DF	M	H	B
Caudofoveata	*Chaetoderma*	CO	L	M	B
Gastropoda	*Tachyrhynchus erosus*	F	L	M	S
Gastropoda	*Cylichna sp. cf. alba*	C	M	M	S
Gastropoda	*Philinoidea*	C	M	M	S
Gastropoda	*Retusa obtusa*	C	M	M	S
Gastropoda	*Heterobranchia*	C	M	M	S
Gastropoda	*Pyramidelloidea*	O	M	M	S
Gastropoda	*Buccinidae*	C	L	M	S
Gastropoda	*Gastropoda*	D	M	M	S
Scaphopoda	*Scaphopoda*	C	M	H	B
Nematoda	*Nematodes*	S	S	M	G
Nemertea	*Nemerti*	C	L	M	S
Demospongiae	*Demospongiae*	F	M	S	S
Sipuncula	*Sipunculida*	D	M	M	T
	Foraminifera	D	S	S	S

Table S4.2: Sediment pigment concentrations (Chl *a* and phaeopigments 'Phaeo'), community descriptors (taxonomic richness S_{Tax}, total abundance N, functional group richness S_{Func} and Shannon-Wiener Index H'_{Func}) and abiotic variables used in the study.

Regime	Site	Year	Chl *a* [$\mu g\ g^{-1}$]	Phaeo [$\mu g\ g^{-1}$]	S_{Tax}	N [ind.]	S_{Func}	H'_{Func}	Depth [m]	Ice-melt [d_{Julian}]
Hotspots	MD-C	2008	23.33	36.44	31	129	23	2.67	45	161
			14.25	31.96	20	172	16	2.25	45	161
			32.44	43.58	32	142	24	2.57	45	161
		2009	3.55	16.93	25	89	19	1.82	47	160
			3.82	9.15	15	75	14	1.84	47	160
			3.89	10.92	19	96	16	2.09	47	160
	AG-CW	2008	0.53	14.66	22	53	16	2.38	206	182
			1.11	15.43	28	98	21	2.11	206	182
			0.87	15.30	24	89	18	1.74	206	182
		2009	1.37	10.81	30	55	19	2.63	154	202
			0.90	10.71	28	87	23	2.67	154	202
			0.79	12.06	23	60	18	2.60	154	202
	LS-W	2008	18.29	37.72	41	186	32	2.59	353	217
			14.02	43.00	34	155	24	2.50	353	217
			10.11	40.82	45	197	31	2.62	353	217
		2009	6.92	33.98	42	253	29	1.95	331	146
			3.57	18.04	36	262	25	1.93	331	146
			4.55	23.68	33	274	23	1.78	331	146
	LS-E	2008	3.21	26.74	36	253	25	1.90	707	182
			4.19	33.80	41	361	25	1.77	707	182
			3.33	31.34	29	238	21	1.50	707	182
		2009	2.73	32.27	31	308	20	1.51	786	167
			1.50	21.65	26	485	18	0.85	786	167
			1.40	19.26	28	457	20	0.95	786	167

Table S4.2 continued

	NW-C	2008	3.53	35.34	27	978	19	0.65	444	147
			1.77	12.42	26	996	19	0.77	444	147
			1.88	11.78	18	741	13	0.72	444	147
		2009	3.21	21.71	41	380	25	2.08	451	153
			2.86	22.85	38	566	25	1.51	451	153
			2.98	25.06	40	457	29	1.90	451	153
	NW-E	2008	2.04	14.78	38	356	27	1.33	668	147
			2.51	20.78	33	355	24	1.15	668	147
			2.56	19.37	37	358	27	1.57	668	147
		2009	1.43	25.64	25	434	17	0.93	669	177
			1.08	19.24	24	339	20	1.18	669	177
			0.68	15.57	28	359	22	1.07	669	177
Coldspots	MS-C	2008	0.43	7.10	28	94	22	2.00	318	175
			0.38	6.98	27	74	19	2.23	318	175
			0.50	6.41	16	78	15	1.35	318	175
		2009	0.04	1.27	10	427	9	0.24	577	216
			0.08	2.24	13	449	12	0.27	577	216
			0.04	1.87	10	407	8	0.18	577	216
	AG-CC	2008	0.09	6.84	9	220	9	0.29	596	161
			0.14	6.77	12	173	10	0.47	596	161
			0.22	7.65	15	244	12	0.52	596	161
		2009	0.17	3.31	9	174	9	0.36	559	195
			0.21	3.48	7	212	6	0.20	559	195
			0.21	4.24	8	204	8	0.22	559	195
	BB-N	2008	0.18	3.63	18	409	15	0.40	795	203
			0.06	4.28	16	403	15	0.40	795	203
			0.14	3.78	16	463	14	0.37	795	203
		2009	0.93	4.54	17	402	16	0.52	810	160
			0.42	3.19	18	274	15	0.52	810	160
			0.39	2.00	15	242	12	0.59	810	160

CONCLUSION

The general objective of my thesis was to provide a description and enhance the understanding of benthic ecosystem functioning and its determining factors at hotspots and coldspots in the Canadian Arctic. Only if we know where the areas are that are important for marine ecosystems' functions, and how they vary naturally, we can assess the impact of climate change and human activities on our environment. As long as we do not know the extent of natural variation (or oscillation), it will be difficult to predict long-term trends.

In the vast and remote Canadian Arctic marine ecosystems, information on life and processes at the seafloor is scarce and we often have to rely on interpretation, as opposed to observations, if the benthic function of an area needs to be evaluated. It is therefore a central interest to find parameters that can provide reliable estimations of benthic ecosystem function. In this study, I focused on the benthic remineralisation as an important component of ecosystem functioning, which interacts with the overall biogeochemical cycles of the oceans. I looked for parameters in the biotic and abiotic environment that can predict benthic remineralisation, and studied where higher and lower benthic remineralisation is found. It was important to assess benthic remineralisation on different temporal and spatial scales to gain a better knowledge and representation of the natural variability. Moreover, I studied how such variability can differ between hot- and coldspots of benthic remineralisation to better assess their reliability as potential sentinel sites of change.

First comprehensive analysis of spatio-temporal variation in benthic remineralisation across the Canadian Arctic shelves

This study allowed for the first time to assess synchronous remineralisation of oxygen and multiple nutrients at the seafloor in the Arctic. I showed that the typically used measure for benthic activity - sediment oxygen demand - is not statistically related to and hence, does not represent the spatial or temporal variation in all other nutrient release or uptake rates (chapitre 2, 3, 4). This implies that the evaluataion, where important seafloor areas for global biogeochemical cycles are, needs to include a subset of multiple benthic flux measures. From a chemical point of view, it may seem more appropriate to calculate carbon, nutrient and oxygen flux budgets separately for each flux. Parts of my results have already served to provide a detailed assessment of carbon cycling in the Amundsen Gulf (Forest et al., 2011). Although data from this thesis may be used for such global flux budgets, this was not the scope of my study. From an ecological and management perspective, it is more important to designate areas, which will be important to be maintained in a healthy state to support the overall functioning of the ecosystem. Further functions of the seafloor such as biomass production or habitat construction (as by corals) should be included to gain a more complete picture, which benthic areas are most important in providing services to the connected ecosystems. As part of my collaborative work, benthic Ecologically and Biologically Significant Areas (EBSAs) were described based on all of these parameters and more (chapitre 3, Kenchington et al., 2011), but rarely was data on all of these different functions available for a region. Hence, the importance of each described benthic EBSAs for the overall ecosystem could only be partially estimated.

The study approach to sample the same sites at different times (or basically monitoring) also allowed for the separation of spatial variation from temporal variation in benthic remineralisation, benthic community composition and food supply, which is still exceptional data in polar regions.

Although pronounced seasonality in the Arctic ecosystems is a commonly accepted paradigm, the detection of seasonal signals in benthic functions has been less clear (Lepore et al., 2007). This may be due to confounding spatial variability. In chapitre 1 (Link et al., 2011) I demonstrated that benthic activity at five sites increases during the spring-to-summer transition, but also that the total benthic carbon remineralisation was different among these sites. In fact, seasonal changes were much more pronounced at a hotspot site that had been influenced by an upwelling in the same year but almost insignificant at a coldspot (Link et al., 2011, Tremblay et al., 2011). These results highlight two consequences: First, comparing sites sampled in spring with other sites of the same region sampled in summer or fall can lead to wrong conclusions on spatial variability. Second, monitoring seasonal changes at hotspots does not represent the dynamics of an entire region.

This study also provides the first description of interannual variation of benthic remineralisation across the Canadian Arctic (and the Arctic), and to my knowledge no dataset of interannual variation in multiple benthic fluxes of such spatial coverage has been published before. The paucity of long-term time series (Glover et al., 2010) and the logistic difficulties to achieve sampling at the same sites in the same seasons makes interannual comparisons in the Arctic even rarer than seasonal studies on benthic remineralisation. I showed that in the majority of places, benthic remineralisation patterns are different in two different years, but these differences are not necessarily in the same direction at all places (chapitre 4). That means that if we want to evaluate climate related changes in benthic remineralisation relevant for biogeochemical cycles in the Canadian Arctic, we cannot base our conclusions on findings from a single site. Moreover, interannual changes (as seasonal changes) were more pronounced at hotspots than at coldspots (chapitre 4). Up to now, studies that recur in the same regions in the Arctic have focused on hotspot regions with high primary production or generally high biological process rates. Following the high variability that I found on an annual time scale, long-term series will be necessary to distinguish stochastic from progressive change at hotspots (Glover et al., 2010; Grebmeier, 2012). On the Mackenzie Shelf, comparison of benthic remineralisation in 2008 and 2009

with 2004 shows a two-fold increase in 2009, the year of lower fluxes. While this could indicate the tendency of increasing benthic fluxes, the data from other years would be necessary to verify the directional change. I observed a similar pattern for the comparison with oxygen fluxes measured in the North Water Polynya in 1998, 10 years prior to this study (chapitre 3). Coldspots generally showed lower temporal variability in benthic remineralisation, and they could be more appropriate sentinel sites to detect directional change and tipping points (Duarte et al., 2012) of benthic ecosystem functioning in the Arctic. Another important result from the interannual comparison is that hotspot sites remained significantly different from coldspot sites in their remineralisation pattern. Therefore, although the amount and pattern of fluxes vary on an annual time scale, they remain higher at hotspots than at coldspots, underlining the importance of hotspots for the health of the connected ecosystem.

While temporal variation in macrofaunal community composition as well as functional community composition could not be found on the annual time scale, spatial variation separated hotspots clearly from coldspots, but also most of the different sites (chapitre 4), which seem to be grouped according to their regions. The expected lack of temporal signals on an annual time scale indicates that macrobenthic community composition in the Arctic may not be suitable to explain the evident spatio-temporal variation in benthic remineralisation.

The spatio-temporal variation of food supply did not show clear patterns: While total food supply varied among seasons and mostly among years at coldspots, the indicator of fresh food (Chl *a*) rather showed spatial patterns than seasonal patterns (chapitre 1 and 4). But changes were greater at hotspots than at coldspots.

First explicit integrative study on the influence of abiotic environmental parameters, resource availability and diversity on ecosystem function in Arctic benthic systems

Finding the factors that influence benthic ecosystem functions the most was another major goal of my thesis. Although it is widely assumed that the biodiversity of a system is most important for its functioning (Hooper et al., 2012), the results throughout my thesis show the predominant role of fresh food supply for benthic remineralisation in the Canadian Arctic. The sediment Chl *a* concentration explained a major part of spatial variation in benthic carbon remineralisation in spring and summer 2008 (chapitre 1), as well as multiple benthic remineralisation in 2009 in the southeastern Beaufort Sea (chapitre 2), and it also explained variation among hot- and coldspots across the Canadian Arctic across both years (chapitre 4). However, it was never the sole parameter affecting benthic remineralisation, and faunal biomass, taxonomic diversity or bottom water oxygenation could explain part of the variation. This indicates the interplay of several factors for the benthic functions provided by an ecosystem.

The water depth of studied benthic systems is often considered a good proxy of food supply. Pelagic-benthic coupling assumes that the longer the export distance is, the more organic matter is degraded during vertical export. Vertical export of organic matter in ice-covered regions, however, can differ from this pattern due to a particularly rapid sinking primary producer composition (Grebmeier and Barry, 1991; Ardyna et al., 2011). In chapitre 1, I could demonstrate that on a regional scale, water depth could explain parts of spatial variation of benthic carbon mineralisation under low-food conditions in spring, but not after the arrival of the season's food pulse at the seafloor. Chapitre 2 also underlined that the depth related spatial pattern of benthic remineralisation of the different nutrients is skewed by an east-west gradient on a regional scale in summer (Fig. 2.2). Even on the scale of Arctic Canada across two years, water depth could explain only 4 % of multiple benthic flux variation in summer and fall (chapitre 4). From the same study it is particularly interesting to note, that the effect of benthic diversity (richness and abundance) was not correlated to depth. Although the importance of depth as predictive parameter for benthic

remineralisation could increase on longer and more continuous time scales (including all seasons), physical (ice-cover) and biological processes in a dynamic system such as the Arctic are more important determinants of food supply and benthic ecosystem functioning.

Environmental parameters that vary on long time-scales are interesting for ecosystem management models because data from different years of surveys can be combined to build a base of spatial variation estimates. In my more detailed assessment, whether long-term or short-term dynamic environmental parameters influence benthic remineralisation on the freshwater-influenced Mackenzie Shelf, I found that proxies of more recent food supply (sediment pigments) are more important than proxies of more long-term quantity and quality of organic carbon input or physical sediment characteristics (chapitre 2). Even the important spatial differences of terrigenic carbon input were less important than recent food input. On a regional scale, the history of organic carbon input can be helpful to improve the description of spatial variation in benthic remineralisation, but the recent food supply remains the most important environmental parameter in predictive models.

Finally, I could confirm that macrofaunal diversity is an important biotic component controlling benthic remineralisation in Arctic soft-bottom ecosystems. Interestingly, the effect of macrofaunal biomass was not important for carbon remineralisation in spring conditions (chapitre 1), but macrofaunal abundance was important in summer and across the years and the Canadian Arctic (chapitre 1 and 4). The number of species encountered was even more important than abundance, and the presence of a strong gallery-bioturbating species was sufficiently important to be retained as a predictor for multiple benthic fluxes (chapitre 4). The role of macrofauna in modifying conditions for benthic bacterial remineralistion is underlined by these results: Initial macrofaunal decomposition of complex organic matter into bioavailable matter and macrofaunal bioturbation activity may be the controlling mechanisms for bacteria-mediated remineralisation (Michaud et al., 2009; Hunter et al., 2012; Piot, 2012). This conclusion supports that a combination of diversity measures can deliver best results when explaining particularly the spatial variation in benthic remineralisation. While taxonomic richness seems more important than

functional group richness, the identity of one species retained in the model supports the approach to look for species' roles and functions in order to predict ecosystem function. Further analyses of the influence of functional community composition on benthic fluxes in polar environments need to be conducted to pursue the quest for the best diversity measure for predicting ecosystem functions.

I clearly found an interaction of resource availability and diversity on the spatio-temporal pattern of benthic remineralisation. Macrofaunal diversity is an important predictor of benthic remineralisation in times and places where food supply is abundant (chapitre 1 and 4). The influence of food supply could also be the possible explanation for the greater importance of taxonomic richness compared to functional group richness: Statistically, functional richness is more strongly correlated to food supply than taxonomic richness. Hence, in predictive models, more information of food supply and functional group richness is redundant for benthic flux explanation than information of fresh food supply and taxonomic richness.

Overall, my results demonstrate that the diversity-ecosystem function relation in arctic benthic systems strongly depends on resource availability and on the temporal scale considered (Fig. 6). The joint picture of the different chapitre in this thesis, hence, allows answering some questions about benthic function hotspots in the Canadian Arctic.

Where are benthic remineralisation hotspots?

How many remineralisation hotspots do we know in the Canadian Arctic?

I showed that independent from interannual variability, six hotspot sites of benthic remineralisation are found in regions with high biodiversity and/or high fresh food supply, namely in the shallow Mackenzie Shelf and Amundsen Gulf bays, Lancaster Sound and the North Water Polynya. These regions were general hotspots compared to other studied regions in the Canadian Arctic (chapitres 3 and 4).

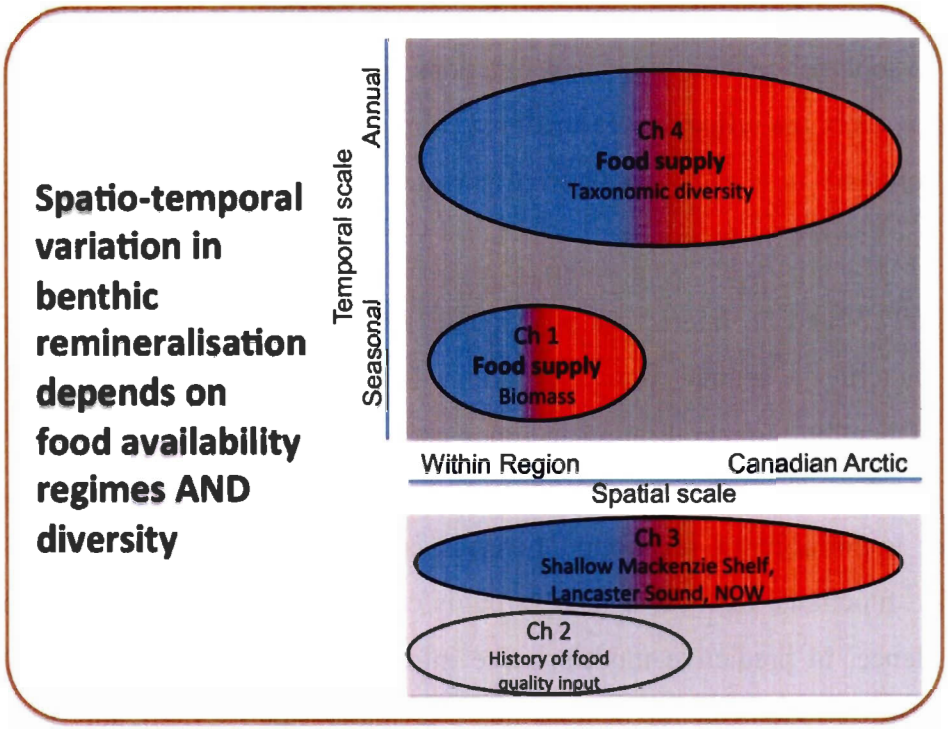

Fig. 6: Overview of the conclusions from the different chapitre (Ch) of my thesis and their link to the overall conclusion. Bubbles present the key factors influencing variation in benthic remineralisation or where the hotspots were found (Ch 3).

How can we find more remineralisation hotspots?

Numerous studies have demonstrated the importance of ice-edges for high productivity in polar regions (Grebmeier, 2012). Based on our results, high primary production does not automatically indicate high benthic ecosystem function (chapitre 3), but polynyas and flaw lead regions did. If observations of high primary production can be coupled with vertical export models and thus estimate the supply of fresh food to the benthos, we have a first indicator of a possible remineralisation hotspot. Nevertheless, the diversity of benthic fauna would be a second, necessary determinant. My results show that taxonomic species richness predicts benthic remineralisation better than functional group richness. But these two diversity measures are correlated, and in case taxonomic diversity measures are doubtful, functional diversity can serve as a proxy. Consequently, more hotspots can be found if we specifically measure functions at sites of high benthic diversity and food supply, starting with polynyas.

Where will remineralisation hotspots be in the future?

Climate effects are rapidly changing the ice-cover and ecosystem dynamics of the Arctic. Some regions may be characterized by higher primary production and vertical matter export due to upwellings (Tremblay et al., 2011), but others may experience higher pelagic matter recycling than before, thus diminishing the food supply to the benthos. Moreover, boreal species are starting to replace arctic benthic species in some regions (Grebmeier, 2012), a trend that might increase due to arctic species' dependence on sea-ice algae (Sun et al., 2009). In the long run, an excess input of organic matter, e.g. on the shallow Mackenzie Shelf, could provoke suboxic conditions and remineralisation patterns of less healthy benthic habitats (Rosenberg et al., 2001). To better estimate the effect of species loss, invasions and shifts, we need to investigate explicitely which benthic community components are most important for benthic remineralisation. It is likely that benthic function hotspots in the future will be at future polynya sites, but we need more knowledge on how benthic communities will change and how they influence benthic functions.

Are hotspots suitable sentinel sites?

The important temporal variation in benthic remineralisation hotspots indicates that long-term series will be necessary to distinguish natural variability from a progressive change in benthic remineralisation. Although coldspots show less natural variability and might therefore be better indicators of change, this assumption could proof to be wrong with data from further years. We cannot say yet, whether observed hotspots are only points in the succession of a respective system, or whether they reflect the characteristics and importance of a region on a longer time scale. Moreover, we should keep in mind that hotspots may not be the only important regions for a global ecosystem function. Areas of particular low processes may also provide extremely rare habitats that can lead to specialized ecosystems, which are important simply due to their uniqueness. I recommend the simultaneous use of hotspots and coldspots to monitor changes in the Arctic marine ecosystems.

Future directions

The conclusions from my thesis answer many questions on the functioning of Arctic benthic systems. But several aspects remain to be studied, and directions for further research on ecosystem functioning emerge.

One aspect that could not be studied to its full extent in the frame of my thesis is the role of the functional identity of species for benthic remineralisation in Arctic marine environments. Although measures of diversity such as species number were helpful to predict variation in benthic remineralisation, there was also evidence of the importance ofbioturbation functions of species. Many studies in intertidal habitats and experimental approaches have demonstrated the importance of particular species traits (mostly bioturbation) for benthic fluxes (Godbold and Solan, 2009; Laverock et al., 2012; Piot, 2012). A first observational study on the importance of species in the natural community for bioturbation and/or remineralisation in arctic shelf sediments can help to determine experimental setups, in which the particular role of single species and their interactions should be determined. Although experimental studies cannot completely represent the complex processes in the natural environment, it is clear that without manipulation of species diversity we cannot estimate the effect of species loss or community shifts in the Arctic.Another component that was not analysed in this thesis is the interaction of the smaller benthic organismal compartment with benthic remineralisation. There is increasing evidence of the role of meiofauna for benthic fluxes (Nascimento et al., 2012; Piot, 2012). Particularly, coldspots of this study showed low macrofaunal abundance and richness, but meiofauna is known to be equally important in hotspots and coldspots such as deep and oligotrophic areas of the Arctic (Kröncke et al., 2000). The influence of bacterial and meiofaunal diversity on spring-time benthic carbon remineralisation in the Arctic has also been demonstrated (Grant et al., 2002; Renaud et al., 2007a), and recent findings stress the role of food quality, i.e., the content and composition of fatty acids, for bacterial remineralisation (Rontani et al., 2012; Tolosa et al., 2012). But Hunter et al. (2012) demonstrated that it is an interactive effect of macrofauna and bacteria activity that

mediates overall phytodetritus degradation (Hunter et al., 2012). The negative effect found for the influence of foraminifera on benthic remineralisation in my study (chapitre 1) also indicates the complex interactions even within the faunal compartment (chapitre 1). Apart from their different metabolism compared to metazoan macrofauna (Pina-Ochoa et al., 2010), their influence on remineralisation could reflect a cascade effect: More foraminifera would consume more bacteria and thus indirectly reduce bacterial remineralisation. Including the smaller organismal compartments into measures of diversity, and gaining a better spatial coverage on the fatty acid quality of benthic food supply, could improve the predictive power of statistical models of benthic remineralisation.

While my study provides a first interannual and a seasonal analysis on benthic remineralisation in the Arctic, we could not yet close the knowledge gap on the annual benthic flux cycle or detect progressive change. Due to the lower productivity outside spring or summer, it is likely that seasonal changes in other transitions (fall-winter, winter-spring) will yield less pronounced changes in benthic remineralisation than the spring-summer transition. However, more studies on seasonal changes across other transitions are necessary to provide annual models of biogeochemical fluxes. Such annual models can then help to calibrate earlier data obtained in different years and different seasons towards an annual mean, and hence add to long-term monitoring series. Permanent seafloor installations in the Arctic to monitor annual remineralisation cycles such as in the VENUS program (http://venus.uvic.ca) could greatly improve our knowledge on temporal variations.

The results of my thesis have been integrated into the regional study of carbon fluxes and pelagic-benthic coupling in the southeastern Beaufort Sea (Forest et al., 2011; Tremblay et al., 2011; Darnis et al., 2012). Such ecosystem-wide understanding of functioning is the key to estimate large-scale impacts of climate change or human activity in the Arctic. Integrating efforts are still necessary for other regions of the Canadian Arctic and the Arctic in general - for pelagic-benthic coupling, but also the benthic-pelagic feedback of nutrient release or biomass production, and eventually the coupling with the

physical processes. The Arctic in Rapid Transition project (ART, Wegner et al., 2011) is a promising initiative with these goals.

Indeed, such integrative studies are also necessary to find common and distinctive drivers of benthic ecosystem function in marine regions of Canada and the world. Benthic remineralisation is one of several goods provided by the seafloor system to the connected ecosystems. Biomass productivity is another benthic function measure, which is important for the food web. Habitat engineering by corals, sponges, bivalves or other sessile species is also a function that enhances an ecosystem's performance by providing niches for associated fauna and thus increasing overall organismal density and diversity (e.g. for mussels, see Largaespada et al., 2012). In a first step, it would be informative to gather data on these different benthic functions and analyse their common patterns in the relation between resource availability and diversity and ecosystem function. In a second step, large-scale experiments including several trophic levels and benthic remineralisation could be conducted in engineered and non-engineered habitats to evaluate the role of biotic bottom structures for ecosystem functioning.

To evaluate the effects of climate change and human activity on polar marine ecosystems it would be ideal to conduct such integrative studies and experiments at sites of long-term monitoring and periodically elsewhere. This way, spatial coverage could be steadily increased, while sentinel sites could calibrate for temporal changes to a certain degree. The increasing number of seafloor observatories is a major step towards this approach, but has not yet reached Arctic shelf environments.

Here, I could decribe hotspots of benthic functions in the Canadian Arctic. A temporally verified decription of benthic remineralisation hotspots in other regions and subsequent comparison of absolute values could provide a relative idea, how important benthic functions in the Arctic are for the world's oceans. A first step in the approach to such large-scale hotspot comparisons is certainly the comparison of Arctic and Antarctic benthic functioning hotspots. Both regions are highly dynamic and subject to be modified with ongoing climate changes. In fact, monitoring the temporal stability of described

hotspots in the Arctic *vs* the Antarctic could provide valuable insights about the pace of climate change effects on our marine ecosystems.

It may also be useful to create a measure of 'functional distinctness', indicating not the quantity, but rather the uniqueness of functions provided by an ecosystem. This could avoid the possibly incomplete conclusion that only sites of elevated functions are important for the overall marine ecosystem functioning and services.

Finally, all scientific research becomes more valuable if we can utilize its findings for sound expert advice to improve governance. Finding the predictive factors of ecosystem functions is only valuable if we can apply the information in ready-to-use tools for stakeholders. My participation in the description of EBSAs in the Canadian Arctic Ocean has been an active step towards integration of (politically) abstract function measures such as benthic remineralisation into baseline information for later management use. This approach provides an example for other marine areas and/or benthic functions, although finding the best proxies will provide an even easier-to-use tool for large spatial planning of sustainable resource use in our marine environments.

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